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INTENSITY REGULATION OF BIOLUMINESCENCE DURING COUNTERSHADING IN LIVING MIDWATER ANIMALS

RICHARD EDWARD YOUNG[1] AND CLYDE F. E. ROPER[2]

ABSTRACT

Nine species of midwater cephalopods, fish, and shrimp, examined in a shipboard aquarium, adjusted the intensity of their luminescence to match the intensity of the overhead light. Most animals tested could regulate this ventral countershading luminescence in response to a wide range of light intensities. A black anglerfish, *Cryptopsaras couesi*, also produced a faint later glow, indicating that bioluminescence may be important in lateral countershading in some species. Our observations indicate that ventral countershading is effective to depths of 750-775 m during the day off Hawaii. We suggest that the concealment strategy of ventral bioluminescent countershading is limited to depths greater than 350-400 m, largely because of the high visual acuity of predators and the high cost of producing countershading luminescence at lesser depths.

In a previous paper (Young and Roper 1976), we demonstrated that the midwater squid *Abraliopsis* sp. turned its photophores on in response to dim overhead illumination in a shipboard aquarium and turned them off when the light was extinguished. In addition, we noted that the squid became invisible from below when the luminescence of the squid had the same apparent intensity as the overhead illumination.

In this paper we examine in more detail bioluminescent countershading in living midwater animals. Tests were conducted on seven species of squids (*Abralia trigonura, Abraliopsis* sp., *Pterygioteuthis microlampas, Pyroteuthis addolux, Enoploteuthis* sp., *Octopoteuthis nielseni, Heteroteuthis hawaiiensis*), one black anglerfish (*Cryptopsaras couesi*), and one half-red shrimp (*Oplophorus gracilirostris*). We will demonstrate that these animals not only respond to on-off sequences of overhead illumination, but alter their luminosity (luminous intensity) in order to match comparable alterations in the overhead illumination. The implications of these and our other findings concerning bioluminescent countershading in the midwater environment are discussed.

Rauther (1927) first suggested that bioluminescent light from the ventrally directed photophores of teleost fishes might diminish their silhouettes when viewed from below. W. D. Clarke (1963) revived the idea and assembled supporting evidence. He suggested that opaque animals in the dimly lit midwaters of the open ocean will be silhouetted against the highly directional downwelling daylight, and they will, therefore, be visible to predators below. The production of downward luminescence of proper intensity would eliminate the silhouette and thereby conceal the animal. Considerable evidence now has accumulated to support the hypothesis of ventral bioluminescent countershading.

Denton et al. (1969) demonstrated that the photophores of the hatchetfish *Argyropelecus* were designed to distribute their luminescence in a manner consistent with countershading requirements. Denton et al. (1970) found that color filters in the photophores of the fishes *Argyropelecus* and *Sternoptyx* passed only blue light at about 480 nm. This wavelength is close to the transmission peak of sunlight in oceanic water. Such "skylight" filters also have been found in a number of squid (Arnold et al. 1974; Young in press), and they probably occur in sergestid shrimps with the photogenic organs of Pesta (Foxton 1972). Young (in press) suggested that all photophores bearing skylight filters were countershading organs. Best and Bone (1976), however, found that photophores with blue color filters are not all directed ventrally in the fish *Xenodermichthys* (and apparently *Photostylus*) and concluded that blue filters must have functions in addition to countershading.

[1]Department of Oceanography, University of Hawaii, Honolulu, HI 96822.
[2]Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

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Young (1973) described extraocular photoreceptors in the midwater squid *Abraliopsis* sp. which seemed designed to detect downwelling sunlight as well as bioluminescent light from some of the animal's own photophores. This system could provide the animal with the information necessary to adjust the intensity of its photophores to match the downwelling light. Similar systems now have been described in a variety of squids (Young in press). Stomiatoid fishes have photophores directed into their eyes that might be a part of a similar system, and Lawry (1974) described a comparable mechanism in myctophid fishes. Arnold et al. (1974) described a possible mechanism for regulating the intensity of luminescence in the countershading photophores of the squid *Pterygioteuthis*.

Several workers have found that data on the vertical distribution of midwater animals support the ventral countershading hypothesis. Badcock (1970) noted a changeover in midwater fishes with increasing depth from predominately reflective species with large ventral photophores to predominately nonreflective species with small or no ventral photophores at a depth of 650 to 700 m off Fuerteventura, eastern Atlantic Ocean. Amesbury (1975) noted similar trends among midwater fishes off Hawaii. Foxton (1970) reported a changeover in the sergestid fauna off Fuerteventura from shallower-living species consisting of half-red shrimps with complex photophores (organs of Pesta) to deeper-living forms with all-red coloration and simple dermal photophores. He suggested that the latter group lived too deeply for countershading to be effective. Walters (1977), in a similar study off Hawaii, pointed out that ventral countershading may be effective 110 to 120 m below a depth where lateral countershading (i.e., countershading of the animal's sides) is no longer of use. While agreeing with Foxton (1970) that the red pigmentation aids in reducing reflection of bioluminescence from nearby animals, Walters suggested that ventral countershading still is necessary in these deep-living shrimps and that the simple dermal photophores are adequate for such low-level luminescence. Walters proposed that the lower limit of ventral countershading off Hawaii is 775 m, the depth where the lower distributional limit of common all-red sergestids with simple photophores approximately coincides with the upper limit of sergestids without photophores.

Young (1973) indicated similar trends in the reduction of photophore complexity with depth in midwater squids and noted (Young in press) that only species living above 700 m had photophores with skylight filters. Habitat data on midwater cephalopods also indicate that bioluminescent countershading may operate at night and at twilight as well as during the day in the open ocean (Young in press). Hastings (1971) suggested that a countershading function in the shallow-water pony fish, *Leiognathus*, was indicated by the luminous radiance pattern and the luminous response to light from a flashlight. If bioluminescent countershading occurs in clear water neritic environments, it probably operates against dim skylight or moonlight at night and not, as Hastings suggested, during the day.

Denton et al. (1972) demonstrated that the angular distribution of bioluminescence produced by the midwater fishes *Argyropelecus* and *Chauliodus* closely matched the radiance field of daylight in the midwaters of the open ocean.

MATERIALS AND METHODS

Animals studied during two 10-day cruises aboard the RV *Kana Keoki* off leeward Oahu, Hawaii, in the spring of 1976 were captured by a shortened version of the 3-m Isaacs-Kidd midwater trawl with a conical, aluminum cod-end bucket. The bucket was designed to reduce internal turbulence and to eliminate strong sunlight. On deck the bucket was wrapped in black plastic during the day and removed to a dark room. At night the catch was brought aboard under dim red light. In both cases the catch was quickly transferred to cold water and live squids were placed in vials with Nitex[3] screening at each end then transferred to holding tanks in a portable lab-van. The lab-van had a light-tight portion with cooled, running seawater and an adjoining dry lab. The temperature in the holding tanks was cycled day and night between 5°-7°C and 15°C to approximate the day-night temperatures in the habitats of the vertically migrating animals. For the most part we had little control over the selection of animals tested. We used only squids that were large enough and in good enough condition for reliable testing. Only one fish and

[3]Use of trade names does not imply product endorsement by the National Marine Fisheries Service, NOAA, or by the authors' institutions.

one shrimp were tested. Although many living specimens of the shrimp were available, time limitations prevented testing more than one specimen.

Tests were made in a tank 30 cm on a side supplied with running seawater. The tank lay inside a black box which supported a series of three Plexiglas light diffusers and a light above the tank, as well as a mirror tilted at a 45° angle beneath the tank. The 25-W light was covered by a Kodak No. 45 blue filter with peak transmission at 487 nm and a range of 430-540 nm. The black box prevented light from entering the tank except from above and from the front observation port. The observation port was draped with a dark cloth which allowed the observer to watch the animals without admitting stray light. The entire apparatus was placed on a vibration dampener which eliminated high-frequency but not low-frequency vibrations. The room in which observations were made was kept dark except for the enclosed overhead light directed into the tank. Observations were made by looking into the mirror beneath the tank at the ventral surface or downward directed aspect of the animal. Prior to each test series, the observer dark adapted for a minimum of 30 min. The squids generally were confined in small screened cages or placed beneath an inverted petri dish held slightly off the bottom to allow water circulation. The small containers enabled better viewing of the animals by restricting their movements but did not seem to affect their responses. The shrimp would not swim upright in the tank, so a supporting harness of monofilament line was tied around the animal at the junction of the thorax and abdomen. The line was suspended from a slender H-shaped float, and a shorter, ballasted line extended below the shrimp. This apparatus held the shrimp in the center of the tank and allowed it to swim in an upright position without noticeably affecting the overhead illumination.

Light measurements were made with an EMI 9558B photomultiplier. A 3.2-mm diameter fiber-optic light guide connected to the photomultiplier was secured in front of the mirror with a narrow crossbar. The entire bottom of the tank was within the acceptance field of the fiber-optic probe. This arrangement allowed the observer a nearly unobstructed view of the mirror and permitted simultaneous measurements of the overhead illumination. A picoammeter connected to the photomultiplier tube was operated by a second person in the adjoining, lighted lab. The light intensity above the tank (overhead illumination) was regulated with a variable transformer by the observer who depended on verbal feedback from the operator in the adjoining lab to set the light at a specific level.

Animals were subjected to the following light regime with only a few exceptions. Light levels were increased in a fixed series of steps by factors of 1, 2, 6.7, 20, 60, 200, and 300 (see Figure 1). A few animals were tested at levels corresponding to factors of 0.5, 0.17, and 0.067 of the step 1 value. Between each step the light was turned off for 10 min. The following regime was used at steps 0.067-3: the light was turned on for 10 min; at the end of 5 min and at the end of the period, measurements of the luminosity of the animal were made. The light was then turned off for 10 min, then the sequence was repeated, providing a total of four trials and four measurements at each step. Initial observations indicated that animals required longer exposures to light at higher light levels, so beyond step 3 the regime was increased to 20-min periods with measurements at 10 and 20 min. The dark time between periods, however, remained at 10 min (the same duration as between steps). Not all animals were subjected to the highest steps. Generally, at a step where the animal's luminosity was equivalent to or lower than its luminosity at the preceding step or when the observer concluded that the animal could no longer match the overhead illumination, the experiment was terminated. Total testing time approached 7 h, including the time given the animal to adjust to the countershading tank. After the highest step,

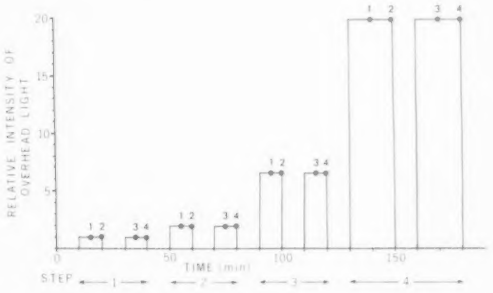

FIGURE 1.—Diagram of steps 1-4 of the testing regime, showing relative light intensities, exposure times during steps, and times (dots) at which countershading measurements were made.

occasionally a lower step was repeated to insure that the animal was still capable of responding. In a few cases, explained in the results, the standard testing sequence was varied slightly.

Measurements of the animal's luminosity at each step were made in the following manner. A luminescing animal, in a natural orientation, was completely invisible when it matched the overhead illumination. The observer quickly reduced the overhead light to nearly zero intensity, then rapidly increased the illumination until the animal became invisible. The observer called the match, and the intensity of the overhead illumination displayed on the current meter was noted by the operator. The measurements, therefore, represent the intensity of the overhead illumination which the animal was judged to be matching, and they provide an indirect measure of the animal's luminosity. As this technique lacks high precision, the four measurements at each step were averaged. The averaging has the disadvantage of combining readings on a squid that did not match the overhead illumination with readings that did match. Since an animal rarely became brighter than the overhead illumination, the effect of averaging usually reduces somewhat the final value of the luminosity of the animal or underestimates the animal's ability to match the overhead illumination. To determine the accuracy of this method, we examined 17 steps in which the animal matched the overhead illumination just prior to the measurement in at least three of the four trials. After the measurements the values for trials within each step were averaged. If accuracy were perfect, these values would be equal to the standard value of the respective step. The actual values in 70% of the cases were within 15% of the standard value of the respective step. Over 75% of the measured values were less than the standard values. Two difficulties contributed to this. When the overhead illumination was quickly increased for a matching reading and the animal started to become invisible against the overhead light, the exact point of disappearance became somewhat subjective, and the observer tended to call for the measurement before disappearance was complete. In addition, an animal occasionally began to lower its intensity immediately when the overhead illumination decreased, but before the measurement could be completed.

On the basis of this analysis, each measurement was assigned a nominal value that was a multiple of 30% of the standard value of the overhead illumination at a given step. Thus, if the measurement was over or under a nominal value by less than 15% it was assigned this nominal value. If the measurement was over or under by more than 15%, it was assigned the next upper or lower nominal value. Both methods of averaging and of assignment into nominal values tended to underestimate an animal's ability to match the overhead illumination. The most critical measure of an animal's ability to match the overhead illumination was the observer's visual determination that the animal was or was not matching just prior to a measurement.

This technique had strong limitations beyond the step at which the animal appeared to match the overhead illumination. Because of increased resolution the observer saw a silhouette with glowing photophores superimposed and he attempted to match the photophore luminosity with the overhead light intensity without losing sight of the silhouette. Such measurements became very subjective. In addition, at high light levels cone vision by the observer becomes significant and would compound any color mismatch between photophore and overhead light. Thus, beyond the level at which the animal matched the overhead illumination, the data were interpreted as an indication only of increase or decrease in luminosity from the previous step.

An animal was recorded to have turned off its photophores during dark periods when luminescence could no longer be detected by the observer (i.e., when the animal's luminosity decreased below the visual threshold of the observer).

We currently are unable to determine the oceanic depths to which our measurements correspond because we have been unable to confidently calibrate our light-measuring system. Our calculations of the energy cost of bioluminescence are based on light values in the ocean near Hawaii at lat. 19°44.5′N, long. 154°40.7′W (E. Kampa pers. commun.).

RESULTS

Enoploteuthidae

Abralia trigonura Berry, 1913

This species possesses numerous photophores of three basic types that are scattered over the ventral surfaces of the body, head, funnel, and arms; in addition, a series of photophores lies on the

ventral surface of each eyeball. This species occupies depths primarily between 450 and 560 m during the day and between 50 and 100 m at night (Young[4]). Four specimens were tested ranging from 28 to 37 mm ML (mantle length).

Three individuals matched the overhead illumination perfectly at most trials in steps 1 through 4, while one specimen did not quite match at step 3. At step 5, one specimen came very close to matching during one trial. While the other individuals could not match this level, they increased the intensity of their luminescence at step 5. The specimen that produced the highest luminosity had been brought through the first three steps at a rapid rate by eliminating two trials at each step. Only one of the two squid tested at step 6 increased the intensity of its photophores at this level; however, it could not begin to eliminate its silhouette at this step or subsequent higher steps. This resulted partly from the increased resolution in the observer's eyes at the high light level; individual photophores and the silhouette could be seen at the same time.

The squid extinguished their lights when the overhead illumination was turned off during the first four steps. Beginning at step 5, two specimens did not extinguish their lights completely during dark periods but always reduced their luminosity to a very low value (average intensity = 35% of the intensity at step 1). Two specimens continued to extinguish their luminescence through steps 6 and 7, but at these high light intensities our eyes began to lose dark adaptation which raised the intensity of the "turn-off" point. At steps 1 and 2 most specimens extinguished their luminescence within 2½ min after the overhead light was turned off, while beyond step 3 extinction times rose to 5 to 10 min. Turn-on times of the photophores following illumination of the overhead light were subjectively determined as the time when the silhouette began to fade. The average time for initial observation of luminescence through step 4 for three specimens was about 1½ min. In several cases initial luminescence was detected within ½ min after the overhead light was turned on.

A large complement of photophores of two different intensities was detected at step 6 through step 8. While the intensity of the dimmer photophores remained the same or decreased slightly at step 8 (see Table 1), the less numerous bright photophores increased in intensity at step 8. Ocular photophores seemed to luminesce at steps 4 and 5 in two specimens; however, these photophores were not detected in the other two specimens.

Abraliopsis sp.

This species has numerous, small photophores

[4] Young, R. E. Photosensitive vesicles and the vertical distribution of pelagic cephalopods off Oahu, Hawaii. Manuscr.

TABLE 1.—Bioluminescent response of midwater animals to overhead illumination. Testing regime included periods of darkness both between and during steps (see text) which are not indicated on chart. Step = category of each test level. Relative light value = intensity of overhead illumination relative to step 1. Matching values = measure of luminescent intensity of animals relative to step 1 in response to the overhead illumination. Solid bar = highest level at which animal was able to match overhead illumination during at least one of the four trials. Dotted bar = highest level at which animal was nearly able to match overhead illumination during at least one of the four trials. Superscripts = number of trials other than the standard four. Parentheses = relative light value of overhead illumination instead of standard step value. + = animal luminesced but measurement not possible. Series 2 = repeat of tests.

Step no.	Relative light value	*Abralia trigonura*	*Abralia trigonura*	*Abralia trigonura*	*Abralia trigonura*	*Abraliopsis* sp.	*Abraliopsis* sp.	*Pyroteuthis addolux*	*Pyroteuthis addolux*	*Pterygioteuthis microlampas*	Series 2	*Octopoteuthis nielseni*	*Heteroteuthis hawaiiensis*	*Cryptopsaras couesi*	*Oplophorus gracilirostris*	Series 2
		Matching values														
0.067	0.067											+				
0.17	0.17											0.20				
0.5	0.5															0.5
1	1.0	1.0	0.72[1]	1.0	0.72	1.0	1.0	0.12[1]		1.0		4.8	1.5		1.5	0.72[2]
2	2.0	2.0	2.0[2]	1.5	2.0	2.5	1.5	1.0		2.0		3.5	1.5	(1.7)2.0	1.5	2.0[2]
3	6.7	4.8	6.7[2]	4.8	6.7	4.8	4.8	3.5	3.5	4.8		10	6.7	7.5	3.5	
4	20	20	20	14	20	10	14	20	14	20		14	20	14[2]	1.5	
5	60	31	43	31	20	(33)20	43	43		60	43[2]	4.8	31			
6	120		75	60		10	43	31		4.8[2]	60					
7	200		75							1.0[2]	4.8[2]					
8	300		60													

of three basic types scattered over the ventral surfaces of the mantle, head, funnel, and arms (Figure 2). In addition a series of photophores lies on the ventral surface of each eyeball. *Abraliopsis* sp. occurs primarily between 500 and 600 m during the day (although it has been captured rarely at depths up to 400 m) and between 50 and 100 m at night (Young see footnote 4).

Two specimens were tested (18 and about 20 mm ML), but they were treated somewhat differently. One squid was tested through six steps with only two trials at each step, then the sequence was repeated through step 5. In both series the step 5 overhead illumination was only 56% of the standard value at this level, so the fifth level is called step 4½ for this specimen. There were no important differences in the animal's luminous responses between the two series and they are combined in Table 1. The second specimen was tested in the standard manner.

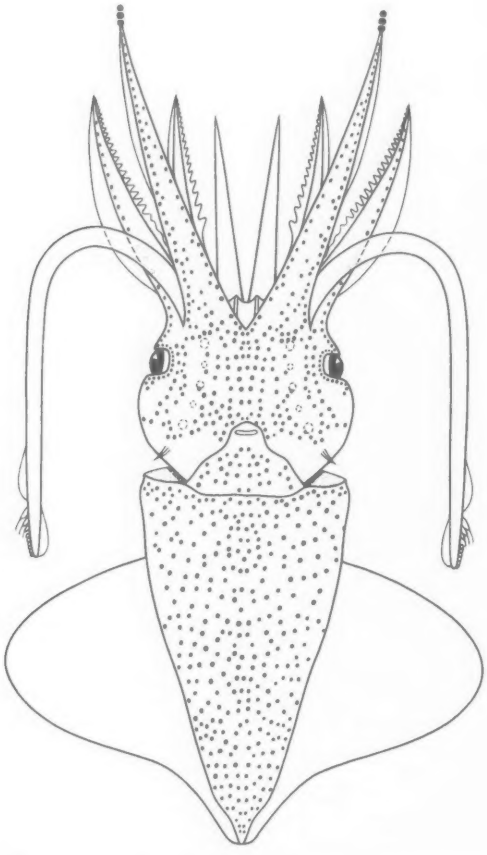

FIGURE 2.—Arrangement of photophores on ventral surface of *Abraliopsis* sp. (from Young and Roper 1976).

Perfect matches were recorded during trials at steps 1 through 4; although one specimen did not match at step 4, it produced a near-match at step 4½. One specimen was able to match the overhead light at step 5 with the observer 1.5 m back from the mirror, while at step 6 a silhouette was still visible when viewed from this distance. Each specimen extinguished its photophores only once during dark periods; however, their luminosity always decreased markedly during these periods. The average luminosity for all trials at the ends of dark periods was 45% of the step 1 intensity.

At least three types of photophores seemed to be involved in countershading at various light levels. Ocular photophores in one specimen seemed to be lighted first at step 4 and were clearly lit at step 4½, but they were never detected in the other specimen. Large numbers of photophores of two different intensities were first detected at step 4 and were apparent at steps 5 and 6. Individual photophores could be detected at step 4 but they could not be resolved with the observer 30 to 45 cm away from the mirror.

Pterygioteuthis microlampas Berry, 1913

This species carries an array of complex photophores on each eye (see Arnold et al. 1974; Young in press) and an equally complex pair in the mantle cavity near the anus. A series of four photophores is located farther posteriorly along the ventral midline in the mantle cavity. The midline photophores have a simpler structure than the others (Chun 1910). Photophores are also present at the bases of the gills and in the tentacles, but they play no role in countershading. *Pterygioteuthis microlampas* lives primarily between 450 and 500 m during the day and 50 and 100 m at night (Young see footnote 4).

One specimen (20 mm ML) was tested. Since this species orients obliquely to countershade (Young in press), a small cage was made to hold the specimen at approximately the correct angle; however, the animal rested on the bottom of the tank with its head tilted more than the body, and the arms were improperly held. Because of the imperfect orientation, the animal was not observed to disappear against the overhead illumination. However, with allowance for orientation, the observer concluded that the squid completely

matched the overhead illumination at each level through step 4, and this interpretation was confirmed by the measurements. By mistake, step 7 was run between steps 4 and 5, so at the completion of the test series, steps 5 through 7 were repeated. The jump from step 4 to step 7 in the first sequence resulted in almost no luminous response from the squid; its luminosity was only that of step 1. The squid came close to matching at the following step 5, but a dim silhouette could be detected by the observer 1.5 m from the mirror. At level 6 the squid again barely responded to the overhead illumination. The squid came even closer to matching the overhead light during one trial of the rerun of step 5. At step 6 in the second sequence, the squid responded to the overhead illumination but could not come close to matching it. Indeed, only a few of the brightest photophores could be detected. The squid barely responded at step 7.

The squid extinguished its lights during three of the four dark periods in steps 1 and 2, and in the remaining steps the luminosity always diminished greatly. The average value of the luminosity by the end of the dark periods was 50% of the step 1 intensity.

Individual photophores could be resolved at step 3, and at step 4, ocular, anal, and one of the midline photophores were visible. The midline photophore was not visible at the beginning of step 5 but was clearly visible by the end of the step. An additional midline photophore was visible at step 6. Some of the photophores were markedly brighter than the overhead illumination at step 5, and at step 6 some of the brightest photophores seemed equivalent in intensity to the overhead light.

Pyroteuthis addolux Young, 1972

This species has nearly the same complement of photophores as the closely related *Pterygioteuthis microlampas*. *Pyroteuthis addolux* occurs primarily between depths of 450 and 500 m during the day and between 150 and 200 m at night (Young see footnote 4).

Two specimens (21 and 23 mm ML) were tested, although we were able to test only one specimen through the entire series. Like *Pterygioteuthis*, *Pyroteuthis* appears to countershade normally in an oblique position. We placed the specimens in a small, bottomless cage to hold them at approximately the proper angle, but they were never well oriented and observations were difficult. Nevertheless, we were able to secure measurements from portions of the animals. Neither specimen performed well at step 1. One specimen was increased to step 3 and measurements were obtained at steps 3 and 4 but were discontinued because of poor orientation. The animal clearly responded to the overhead illumination during these two steps but, because of the orientation problem, the observer could not determine whether or not the animal matched the overhead illumination. The second specimen was better oriented, but the sides of the cage cast a shadow at low light levels, making it difficult to determine how well the animal matched the overhead light. In addition, the arms were held slightly away from the body axis exposing a dark silhouette of the large, heavily pigmented buccal membrane. Nevertheless, the data show that the animal was countershading. The observer concluded at step 4 that if the animal were properly oriented it would completely match the overhead light. The animal came close to matching at step 5, but at step 6 the intensity of its photophores was less than at the previous level.

The specimen tested only at steps 3 and 4 extinguished its lights during dark periods. The other specimen extinguished its lights during the dark periods of steps 1 through 3. At steps 4 through 6 its luminosity always decreased greatly during dark periods to an average value equivalent to the light intensity at step 1.

Enoploteuthis sp.

This animal has numerous photophores of two basic types distributed over the ventral surface of the mantle, head, funnel, and arms. The mantle photophores that contain skylight filters have a slightly different distribution than the nonfilter type. They form oblique strips that extend from the ventral midline of the mantle to its lateral margins. A series of photophores also is present on the ventral surface of each eyeball. Based on a few captures, *Enoploteuthis* sp. occurs at depths of 500 to 600 m during the day and in the upper 100 m at night (Young see footnote 4).

A single animal (37 mm ML) was tested before we established a standard testing procedure. The results, therefore, are not included in Table 1. The specimen increased its luminosity as the overhead light was increased from one level to the next, and it reduced its luminescence greatly when the

overhead light was extinguished. The squid matched the overhead illumination at levels comparable to step 1 through step 4½, and at a level comparable to step 5 it nearly matched when the observer was 45 cm from the mirror. The ocular photophores luminesced at a level comparable to step 4 and the oblique strips on the mantle were clearly seen to glow.

Octopoteuthidae

Octopoteuthis nielseni Robson, 1948

This species is a stocky squid with enormous, muscular fins. The animal is heavily pigmented and possesses a small number of widely spaced photophores that, in dissection, have a very simple structure. The photophores that were observed to luminesce on the one specimen tested (70 mm ML) are illustrated in Figure 3. Based on sparse data, Young (see footnote 4) indicated a depth distribution between 650 and 765 m during the day and between 100 and 200 m at night.

The testing sequence differed somewhat for this animal. Testing began at step 1, dropped to step 0.17, and then to step 0.067. Step 1 was repeated, then followed by steps 2 through 6 in the standard procedure. With the observer 30 cm back from the mirror at step 1 the squid came close but did not quite eliminate its silhouette, although the individual photophores were much brighter than the overhead light. The figures in Table 1 reflect matching of individual photophores and not of the animal as a whole. The squid typically folded its fins against its body, and it could countershade more effectively in this attitude. The folded fins reduced the distinctness of some of the photophores. At level 0.17 the squid matched the overhead illumination perfectly when the fins were folded against the body and the observer was 30 cm away from the tank. The overhead light at step 0.067 approached the threshold intensity for the observer and the silhouette of the large squid first appeared as a faint smudge then disappeared. Measurements were not possible because of the extremely low light levels. When the overhead light was extinguished at this step, the squid could be seen to be glowing and the luminescence faded rapidly.

The squid extinguished its photophores during dark periods at steps 0.067 through 1. The specimen diminished greatly in intensity during the dark periods at step 2, but turned upside-down on both occasions before the photophores were extinguished. Photophores were not extinguished at steps 3 through 6 but decreased to an average of 60% of the step 1 intensity by the end of the dark period.

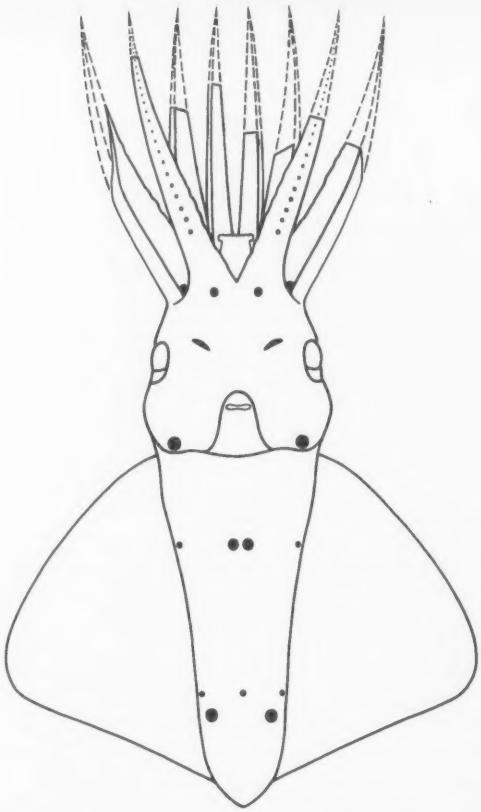

FIGURE 3.—Arrangement of photophores on ventral surface of *Octopoteuthis nielseni*.

The squid was unable to match the overhead light beyond level 0.17; however, it continued to increase the intensity of its photophores through step 4, while at step 5 the intensity decreased greatly. Step 3 was repeated to check the animal's condition and its response was the same as the previous test at that step.

The following photophores were visible at step 1: two large posterior mantle photophores, two ink sac photophores, two photophores at the posterior margin of the head, four photophores at the bases of arms III and IV, and, at the beginning of the

dark period, the axial photophores along the ventral arms. The remaining photophores on the mantle and head were detected at step 3.

Sepiolidae

Heteroteuthis hawaiiensis (Berry, 1909)

This species is a small, robust cephalopod with a single, large photophore embedded in the ink sac (see Young in press). Animals larger than 17 mm ML are found between 375 and 650 m during the day and between 100 and 550 m at night (Young see footnote 4).

A single specimen, 24 mm ML, was tested. *Heteroteuthis hawaiiensis* countershades in an oblique position. Even though the animal was placed in a small cage, the animal's orientation was not perfect. The animal did not countershade well at the first two steps. During this period the squid was upset and discharged luminous clouds several times. The animal nearly matched the overhead illumination at step 3 and did match at step 4. The specimen again was very disturbed during step 5; it discharged luminous clouds and did not match the overhead illumination. The animal extinguished its photophore very rapidly in the dark periods of all five steps.

Ceratiidae

Cryptopsaras couesi Gill, 1883

Only two juvenile specimens of *Cryptosaras couesi* have been taken previously in horizontal tows off Hawaii; both were captured at night at 180 and 195 m (T. A. Clarke pers. commun.). The adult specimen examined here came from a tow that descended to about 200 m at night. Bertelsen (1951) found this species to occupy lesser depths than any other anglerfish examined. Unfortunately, day and night captures were not distinguished. R. H. Gibbs, Jr. (pers. commun.) has taken this species at a minimum depth of 635 m in an opening-closing net during the day in the Atlantic.

The specimen examined was a female, 150 mm standard length, with a small parasitic male attached to its ventral surface. *Cryptopsaras couesi* is a small jet-black anglerfish whose luminescence was thought to be limited to its esca and caruncles. To our vast surprise, this specimen was capable of luminescent countershading. We would not have introduced this animal into our experimental tank had it not been glowing when the catch was sorted. The glow was very directional which suggested a countershading function, although it was directed posteriorly. We could not detect the source of the luminescence, but it appeared to originate from the skin; where the skin was abraded or purposely cut, there was no luminescence. Except for the anteriorly placed, blunt lower jaw, all of the black skin, including that on the fin rays and on the dwarf male, luminesced. After some minutes in a holding tank, the luminescence decreased greatly and the animal was placed in the experimental tank. The fish immediately adopted a head-up position directing the low-intensity glow downward (measured at one-third the intensity of step 1) (Figure 4).

The first test level was set well above step 1 to obtain an unambiguous response. The series, therefore, began at an intensity slightly lower than step 2. When the overhead light was turned on the fish was darkly silhouetted, but it rapidly increased its luminescence until it virtually disappeared from view. It continued to match the overhead illumination perfectly through all trials of step 2. In the initial two trials of step 3 the fish matched the overhead illumination perfectly, while on the last two trials its luminosity was slightly greater than the overhead illumination. While the fish never completely turned off its luminescence during dark periods, it decreased its intensity during step 2 to an average of 10% of the step 1 intensity and during step 3 to an average of 150% of the step 1 intensity. When the lights were extinguished during step 3, and the fish was observed through the side of the tank a faint glow could be seen from its lateral surfaces. The intensity of the glow was comparable to our "ghost stage" (see Young and Roper 1976) which generally measures between 2 and 4% of the intensity of step 1. This estimate indicates that the lateral glow was $^1/_{15}$ to $^1/_{30}$ of the intensity of the ventral glow.

The fish came close to matching the overhead illumination at step 4; but after 10 min the fish discharged luminous material from the caruncles, turned head downward, and beat its tail vigorously for 3 min while its head pressed against the bottom; finally it lay motionless on the bottom. Although the intensity of the overhead illumination was decreased, the fish did not resume the head-up position. The fish was preserved while still alive nearly 2 h later after considerable additional handling and observation.

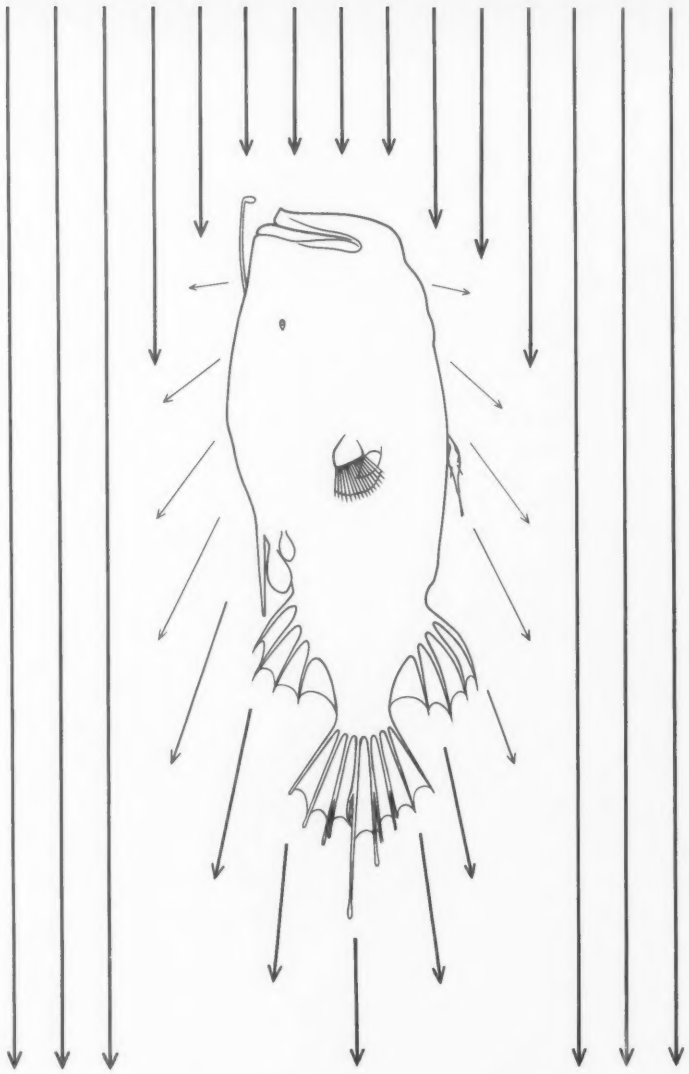

FIGURE 4.—Artist's rendition of luminescent countershading by *Cryptopsaras couesi*. Parallel vertical lines represent downwelling light; lines radiating from fish represent relative luminescence.

Oplophoridae

Oplophorus gracilirostris A. Milne-Edwards, 1881

This species is a half-red shrimp. Photophores that were observed to luminesce occurred on each side of the abdomen, near the joints of the last three thoracic appendages, and on the ventral side of the third maxillipeds. When the thoracic appendages are folded beneath the thorax, the photophores are aligned in two series that are continuous with the two series of photophores along the abdomen (Figure 5). Other photophores are present, but were not observed to luminesce. One specimen, 18 mm carapace length, was examined.

The shrimp matched the overhead illumination perfectly when the thoracic appendages were folded in during trials at steps 1 and 2. The animal, however, was unable to match the overhead illumination at higher steps, even though it clearly increased its luminosity at step 3. At step 4 its luminosity decreased below that at step 3.

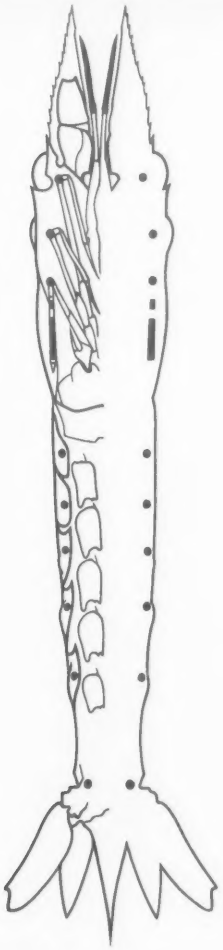

FIGURE 5.—Arrangement of photophores observed to luminesce on ventral surface of *Oplophorus gracilirostris*. (Right half of drawing shows only outline of shrimp and photophores.)

Steps 1 and 2 were repeated and the animal again matched the overhead illumination. The overhead light was then decreased to step 0.5 at which the shrimp also matched perfectly.

Oplophorus gracilirostris turned off its photophores during the dark periods of steps 0.5 through 2. The shrimp reduced its luminescence greatly (average intensity = 5% of the step 1 intensity), but it did not turn off during the first dark periods of steps 3 and 4. During the second dark period in these two steps, the animal's lights were extinguished.

DISCUSSION

Our studies demonstrate that the animals tested turned their photophores on in response to overhead illumination and turned them off or greatly reduced their luminosity when the overhead light was extinguished. The data also show that the animals in experimental tanks can increase and decrease their luminosity to match alterations of the overhead illumination. Further, the data demonstrate that under certain conditions photophores other than those bearing skylight filters can be involved in countershading. Our observations confirm that a luminescing animal disappears from view when it matches the overhead illumination.

The studies also show that bioluminescence can be used for lateral as well as ventral countershading. This was demonstrated by a black anglerfish. A lateral glow was observed from this animal with an intensity estimated to be approximately the value necessary for lateral countershading according to the radiance distribution of daylight in the ocean (Denton et al. 1972).

Black stomiatoids occasionally are captured between 500 and 600 m off Hawaii (T. Clarke 1974), within the realm of the half-red shrimps and the silvery fishes and squids. Black fishes do not reflect light well laterally (Nicol 1958), suggesting that they cannot countershade well at this angle. Even though some of these fishes have a slight lateral bronze iridescence, this iridescence reflects blue light well only at oblique angles (Denton et al. 1972). Such animals seemingly would be conspicuous at 500 to 600 m in the ocean where lateral countershading typically is required. Many of these black fishes also have numerous small photophores along their flanks, indicating that they may utilize bioluminescence for lateral countershading. Perhaps silvery fishes rely totally on reflected light for lateral countershading, while black fishes (at depths where lateral countershading is necessary) rely to varying degrees on bioluminescence. While the latter strategy is energetically more expensive, it has the advantage of simultaneously camouflaging the animal against downwelling light and the flashes or searchlights of nearby animals.

The animals tested matched light intensities indicative of their relative depth range during the day. Midwater animals that occur as near the surface as 450 m during the day (i.e., *Abralia trigonura*, *Abraliopsis* sp., *Pterygioteuthis micro-*

lampas, Pyroteuthis addolux, Heteroteuthis hawaiiensis, and probably *Enoploteuthis* sp.) were able to countershade at step 4 and, in some cases, nearly at step 5. *Oplophorus gracilirostris,* which has an upper distributional limit of 490 m (Zieman 1975), countershaded at step 2 but not at step 3. *Octopoteuthis nielseni,* which has not been captured at less than 650 m off Hawaii during the day, could not quite match the overhead illumination at step 1, but it could countershade effectively at the lower intensities of steps 0.17 and 0.067. The black anglerfish countershades at light intensities at step 3. Although one specimen has been taken at a depth of 635 m, the upper limit of the day habitat of this species is uncertain.

Bioluminescent countershading must have upper and lower depth limits beyond which it no longer is effective. We are unable to determine the depths in the ocean to which the light intensities in our experimental system correspond. We believe, however, that the maximum intensity at which the animals can effectively countershade corresponds approximately to that of the upper limit of their day habitat. For several of the species examined this depth is 375 to 400 m (Young 1977). Our observations indicate the critical role that increased resolution at these depths plays in the effectiveness of countershading. During testing at these high light levels, individual photophores often could be resolved and the outline of the silhouette of the animal became distinct. While resolution of the observer's eyes (and presumably those of a predator) increases with increasing light levels, at these higher intensities resolution becomes so acute that luminescent countershading becomes an extremely difficult task for the animals. This strategy remains effective only at increasingly greater distances from the countershading animal.

The energy required to countershade at less than 400 m must also affect the utility of this strategy. We have made rough calculations of this cost based on one of the squid tested (*Abralia trigonura*) with a silhouette of 4 cm^2 and a wet weight of 2.5 g. At 400 m off Hawaii during the day, this animal must produce a light flux in the range of 0.9×10^{16} quanta/h in order to countershade. In the absence of data on cephalopods,[5] we assume the squid has a luminescent system similar to the firefly in which 60 kcal/mole is required to obtain an excited state of the luciferin molecule (McElroy and Seliger 1961). Since the quantum yield is about unity, this figure corresponds to 60 kcal for the production of 6.022×10^{23} quanta (Avogadro's number). Therefore, 0.0009 cal is necessary to produce the required number of quanta at 400 m. Unfortunately, very little is known of the energy budget of midwater squids. Belman[6], however, reported oxygen consumption of 0.030 μl O_2/mg wet weight per h in the midwater squid *Histioteuthis heteropsis* at 5°C. (Childress (1975) gave rates of 0.006 to 0.011 (average 0.035) μl O_2/mg wet weight per h for a variety of midwater shrimp at temperatures between 4° and 7.5°C.) Using the average energy equivalents of oxygen consumption in carnivorous ammoniotelic animals of 3.24 cal/mg O_2 consumed (Elliott and Davison 1975), the energy required for countershading at 400 m by this squid is 0.3% of the energy consumed by the resting animal during the day. Since downwelling light intensity changes by a factor of approximately 30 per 100 m near Hawaii (k = 0.034), at 350 m the cost of countershading climbs to 1.6%, at 300 m it becomes 9%, and at 200 m it becomes 270%. These figures would increase by a factor of over 3 if we based the energy costs on the luminescent system of the ostracod *Cypridina* rather than that of the firefly (Shimomura and Johnson 1970). The limitations imposed on bioluminescent countershading apparently above 350-400 m by the apparent high visual acuity of predators and by the high energy costs, suggest that few animals are capable of countershading above these depths during the day.

Walters (1977) suggested that the lower limit for ventral countershading off Hawaii is about 775 m, based on the assumption that simple photophores in all-red sergestids are used for countershading. Our observations on countershading in *Octopoteuthis nielseni,* which has simple photophores, supports his assumption. In addition, we were able to detect the silhouette of *O. nielseni* at step 0.067, but we could not detect it with the overhead intensity reduced again in half. If we compensate for the distance of the observer from the specimen and the light loss in the mirror, our

[5]Recent estimates of activation energy and quantum yield by the flashing photophore of an epipelagic squid indicate a very high metabolic cost (Girsch et al. 1976) that presumably is not applicable to countershading luminescence.

[6]Belman, B. W. Respiration and the effects of pressure on the vertically migrating squid *Histioteuthis heteropsis.* Manuscr.

threshold would be about this latter intensity, or approximately 0.06% of the intensity at step 5. If we assume that light intensities at 400 m off Hawaii correspond to light intensities midway between steps 4 and 5, the depth of our visual threshold for detecting large silhouettes would be about 610 m. Denton and Warren (1957) suggested that the eyes of deep-sea fishes are 60 to 120 times more sensitive than the human eye. These figures indicate that a fish should have a visual threshold for detecting silhouettes somewhere between depths of 730 to 750 m.

At the greatest depths where ventral countershading occurs, simple photophores suffice (e.g., *Octopoteuthis nielseni*); however, at higher light levels photophores often possess skylight filters (e.g., *Abralia trigonura, Abraliopsis* sp., *Pyroteuthis addolux, Pterygioteuthis microlampas, Enoploteuthis* sp., *Heteroteuthis hawaiiensis*).Skylight filters on photophores apparently eliminate the "tails" of spectral emission bands that lie outside the spectral range of downwelling light. Presumably these tails develop or are detectable at high luminescent intensities only. Best and Bone (1976) suggested that not all photophores carrying such filters were involved in countershading. However, in view of the role of bioluminescence in lateral countershading demonstrated here, and the fact that some fishes may countershade in the head-up position (as *Cryptopsaras couesi*), one must be cautious in ruling out a countershading function based on photophore distribution. Indeed, we examined one of the species Bone and Best examined, *Photostylus*, and found that the photophores are clearly directed posteriorly, indicating a head-up countershading orientation. Apparently beyond an animal's normal upper limit of countershading, it may turn on nearly every ventrally directed photophore it possesses in an attempt to eliminate its silhouette, even though some of the photophores lack skylight filters (e.g., *Abralia trigonura, Abraliopsis* sp., *Pyroteuthis addolux, Pterygioteuthis microlampas, Enoploteuthis* sp.).

The evidence in support of the theory of bioluminescent countershading in the midwaters of the open ocean is now substantial. The only major evidence lacking is the experimental demonstration of reduced predation on countershading animals and field observations of the phenomenon. The apparent importance of bioluminescent countershading in midwaters cannot be overestimated. Countershading appears to operate from depths of 750-775 m to about 350-400 m during the day off Hawaii. This zone is inhabited during the day by the great majority of fishes (Amesbury 1975), shrimps (Zieman 1975; Walters 1977; Riggs[7]), and cephalopods (Young see footnote 4) that occur in Hawaiian midwaters. The upper limit of the midwater fauna off Hawaii occurs at approximately 400 m (Maynard et al. 1975; Amesbury 1975). Amesbury (1975) in comparing the upper depth limits of midwater faunas in various areas, concluded that these depths were related to light intensity. We suggest that the upper depth limit of the midwater fauna is a result, to a large degree, of the severe limitations placed on bioluminescent countershading at this level. We envision a changeover in the macrofauna at this depth from a deeper component in which opaque animals are able to hide, to an upper component in which opaque animals must rely more on speed, size, weapons, etc., than on hiding to avoid predation.

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[7]Riggs, F. Vertical distribution of the pelagic shrimps, *Gennadas* and *Bentheogennema* off Oahu, Hawaii. Manuscr.

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FISHERY WASTE EFFLUENTS: A SUGGESTED SYSTEM FOR DETERMINING AND CALCULATING POLLUTANT PARAMETERS

JEFF COLLINS AND RICHARD D. TENNEY[1]

ABSTRACT

An improved and simplified system to test for pollutants in shrimp waste effluents is presented. In addition, two methods were developed to calculate both protein and oil and grease content. The first method is based on establishing empirical regressions of protein or oil and grease on total residue. The second and preferred method, a simultaneous equation, is independent of these correlations but dependent on the total residue and chemical oxygen demand (COD) of the waste effluent obtained through routine analyses. The COD value was found to depend upon the amount of potassium dichromate remaining at the completion of the 2-h reflux period. The dichromate can vary from 0 to 6.25 meq excess and between 2 and 5 meq, the COD will vary 4.2%. A table of factors is given to correct the COD to 3.5 meq excess. Coefficients of COD were determined on a number of preparations of protein and oil and grease from shrimp waste effluent and from fish and shellfish. These coefficients (1.338 mg COD/mg protein and 2.678 mg COD/mg oil and grease) were required for the simultaneous equation. The simple analytical tests and mathematical treatment used in this system would be less expensive to the industry and would result in a more accurate and comprehensive evaluation of the waste load than currently obtainable by methods specified in the monitoring regulations.

An improved testing program for fishery waste effluents has been suggested (Collins and Tenney 1976) in which the total residue (TR) and the chemical oxygen demand of the filterable residue (COD_{FR}) were to be determined by analysis and used to calculate other parameters from equations previously established for a particular plant and process. It was also suggested that the protein and oil and grease (O&G) content could probably be calculated from COD and TR data to give more accurate values than by direct analyses.

The purpose of this study was to test the validity of such a testing-calculating system on waste effluents from a shrimp plant in Kodiak, Alaska. A further purpose was to derive equations whereby O&G and protein could be calculated from COD and TR data.

EXPERIMENTAL

Grab samples were taken at specific times during the shrimp production periods to obtain a range in values that would be useful for subsequent mathematical treatment. Waste effluents were taken from the underflow of a Bauer Hydrasieve[2] (1 mm, 0.04 inch) in a plant processing shrimp with combined Model A and PCA peelers. The methods of analysis and the method of calculating data are similar to those reported previously (Collins and Tenney 1976). The test for filterable residue (FR) was modified, however, to give sufficient filtrate (900 ml) for duplicate macro-Kjeldahl, COD, FR, and ash analyses. About 1,000-ml effluent, after settling 30 min, was decanted through a plug of glass wool in a powder funnel positioned over a 600-ml coarse sintered glass funnel containing GF/A glass filter paper and ¼ inch of dry base-acid-water washed ASTM standard Ottawa sand (C-190). The suction flask was evacuated briefly several times during filtration and clamped off to prevent plugging of the filter and evaporation. We have found that use of continuous evacuation causes rapid plugging of the glass filter paper and, additionally, could cause considerable errors through evaporation.

As will be discussed later, the precision of the residue and ash analyses is particularly important. Consequently, considerable attention was given these analyses to obtain good precision as well as convenience in conducting the analyses. The major steps of the procedure follow:

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

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1. Heat 100-ml Pyrex beakers at 500°C for 1 h, air cool for 1 h, and weigh. Prior to use, new beakers should be equilibrated to ashing conditions.
2. Accurately weigh about an 80-ml sample of effluent into the dry beaker. Dry overnight at 103°C in a forced draft oven and weigh after 1 h of air cooling.
3. Calculate TR in milligrams/liter. (Note: this system, of course, gives TR in milligrams/1,000 g, but we follow the convention and express it in milligrams/liter.)
4. Heat beaker and dried sample at 500°C for 2 h, air cool 1 h, and weigh as before.
5. Calculate ash from the initial weight of sample, express as milligrams/liter as in step 3.

RESULTS

In general, these effluent samples were tested for COD, residue, ash, O&G, and protein. The data in Table 1 are averages of duplicate analyses, except O&G which is in triplicate. The data should not be considered representative of the effluent from this plant because of the specific way of taking these grab samples. Comparisons in relative data, however, can be made. For example, the COD of the filterable residue (COD_{FR}) was slightly over one-half of the total COD (COD_{TR}) and the filterable residue (FR) was 64% of the total residue (TR) on an ash-free basis. The TR contained 17% ash, but most of the ash was found in the FR fraction (92%) leaving only 8% in the nonfilterable residue (NFR) fraction.

The relationship between COD and ash-free residue is plotted in Figure 1 and that for O&G and protein versus ash-free residue is given in Figure 2. The coefficients of correlation were 0.99 and 0.97 for the COD regressions on TR_K and FR_K, respectively. The *F*-test for linearity at the 95% level of significance was 0.015 for the TR_K line and

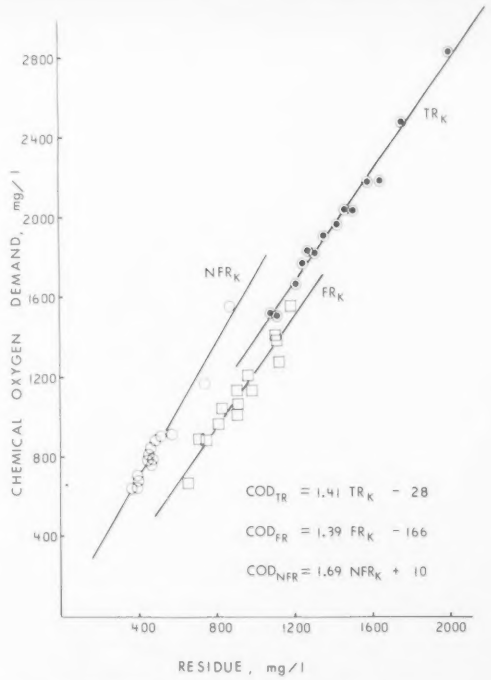

FIGURE 1.—Relationship between the COD and the concentration of the ash-free residue in waste effluents from a plant using both Model A and PCA peelers and fresh water.

TABLE 1.—Analyses of screened shrimp waste effluents from a plant using both Model A and PCA mechanical peelers. [All values in milligrams/liter.]

Sample number	Chemical oxygen demand		Residue		Ash		Protein (6.25N)		Oil and grease
	TR	FR	TR	FR	TR	FR	TR	FR	TR
1	1,517	672	1,420	946	304	291	831	522	185
2	2,839	1,280	2,328	1,441	325	310	1,319	859	486
3	2,190	1,016	1,911	1,146	264	241	1,215	785	276
4	2,182	1,413	1,897	1,400	308	288	1,281	947	258
5	1,824	1,139	1,567	1,146	261	242	1,056	790	203
6	1,917	1,210	1,602	1,182	242	220	1,075	806	230
7	2,039	1,393	1,833	1,418	324	298	1,212	944	229
8	1,771	964	1,532	1,061	280	256	1,037	744	195
9	2,481	1,565	2,137	1,522	378	332	1,425	1,072	302
10	1,969	1,066	1,750	1,197	321	284	1,175	835	204
11	1,666	883	1,460	965	247	224	1,025	703	186
12	1,829	1,046	1,573	1,093	286	263	1,116	794	175
13	2,041	1,156	1,822	1,310	352	328	1,188	863	233
14	1,522	883	1,351	946	256	228	925	644	148
Mean	1,985	1,120	1,727	1,198	296	272	1,134	808	236
SD	361	240	280	193	41	38	158	136	83

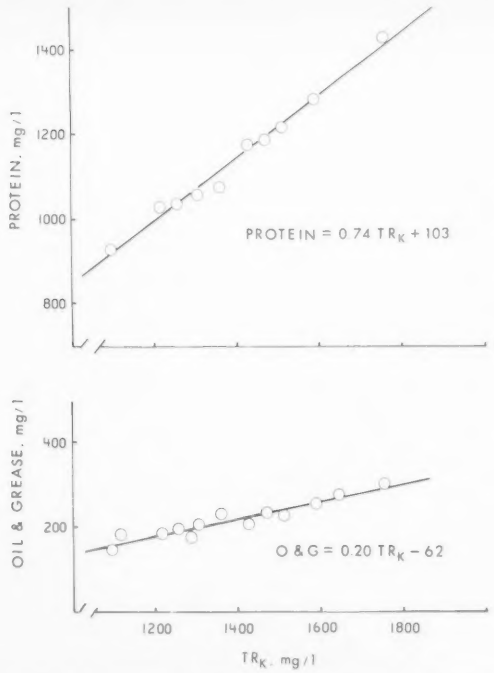

FIGURE 2.—Relationship between the concentration of protein or oil and grease and the concentration of the ash-free total residue in waste effluents from a plant using both Model A and PCA peelers and fresh water.

0.068 for FR_K. The regression lines and equations found in Figures 1 and 2 include a correction for ash content in the residue, i.e., TR − ash = TR_K. These equations, obtained by the method of least squares, are as follows:

$$COD_{TR} = 1.41\ TR_K - 28 \quad (1)$$
$$COD_{FR} = 1.39\ FR_K - 166 \quad (2)$$
$$COD_{NFR} = 1.69\ NFR_K + 10 \quad (3)$$
$$\text{Protein} = 0.74\ TR_K + 103 \quad (4)$$
$$O\&G = 0.20\ TR_K - 62 \quad (5)$$

In our previous paper we suggested that background data for a particular plant should be determined [Equations (1), (2), and (3)] so that the other parameters could be calculated from routine tests for TR and COD_{FR}. Since usage of salt and seawater in plants tends to vary, we now also suggest that an ash analysis be done to eliminate variability in the total residue. Once background data have been established for a particular plant or product process, our testing-calculating system would proceed as follows: Determine TR and ash and substitute the difference into Equation (1) and solve for COD_{TR}. Using the mean values for TR and ash of Table 1 gives 1,431 mg/liter TR_K. Substitution into Equation (1) gives 1,990 mg COD_{TR}/liter which nearly agrees with the mean analytical COD value. Similarly, the other recommended routine test for COD of the filtrate (COD_{FR}) gives a mean value from Table 1 of 1,120 mg/liter which, when substituted into Equation (2), gives 925 mg/liter for FR_K, in agreement with the difference between FR and ash, i.e., FR − ash = 926 mg/liter. The NFR or COD_{NFR} are obtained by difference, e.g., $TR_K - FR_K = NFR_K$. In order to calculate protein and O&G, the TR_K can be substituted into Equations (4) and (5). A rough estimate of O&G content can also be obtained by dividing the COD by 9 which is the average for the ratio of COD to the weight of O&G. The ratio actually varies from about 8 to 10 and inversely with the COD. The ratio and equations only have application to this plant and processing conditions. For other processing conditions or plants, the baseline data and equations should be determined in the same manner.

CALCULATION OF O&G AND PROTEIN USING A SIMULTANEOUS EQUATION

In this section we will derive a simultaneous equation that can be used as a substitute for direct analysis so that O&G and protein can be calculated by using routine data on COD_{FR}, TR, and ash. The equation is based on the assumption that the sum of the COD of each component in the effluent equals the total COD, i.e., COD ($x_1 + x_2 \ldots x_n$) = total COD; and that the sum of the weights of each constituent having an effect on COD equals the total residue minus ash, i.e., Residue ($x_1 + x_2 \ldots x_n$) = Total residue − ash.

To develop the simultaneous equation, coefficients must first be determined that relate COD to the two major constituents of a fishery waste (protein and O&G). In addition, the residue-ash relation needs defining.

COD in Relation to Protein and O&G

To establish a relationship between COD and pollutants, we prepared samples of protein and

O&G and determined their COD equivalent by direct analysis.

To prepare protein a sample of muscle was washed with water and centrifuged to remove the blood and other small nitrogen components, then washed with 2-propanol (IPA) to remove part of the water. The sample was blended and refluxed twice with IPA followed by filtration, washing, and refluxing with petroleum ether (PE) and overnight drying at 103°C. These oil free, white, odorless protein samples were analyzed for nitrogen by the standard macro-Kjeldahl method (Horwitz 1965:273) and for COD. The COD factor was calculated on a 100% protein basis.

To obtain O&G, the sample of fish or shellfish was briefly rinsed with water and IPA; then, using a high speed blender and anhydrous conditions ($MgSO_4$), the O&G was extracted, cold, with IPA and PE. For waste effluent, O&G was obtained by the analytical method used previously (Collins 1976). By either method, after weighing the dry O&G and diluting to volume with PE an aliquot of the final solution equivalent to 8-10 mg O&G was evaporated in the COD flask, oven-dried for 0.5 h, and used for COD determination. Since PE has a residue significantly affecting COD, freshly distilled PE was used throughout the tests.

The COD equivalent was determined on a number of different preparations of O&G and protein from fish and shellfish muscle and from shrimp waste effluent. The average values of from 5 to 30 replicate COD analyses for each material are given in Table 2.

The COD coefficients for protein are in reasonable agreement and are probably independent of species or product form. The theoretical COD coefficient of protein was calculated using amino acid percentage composition data for snow crab reported by Krzeczkowski and Stone (1974). The theoretical figure of 1.285 mg COD/mg protein was in close agreement with our experimental figure of 1.338. The coefficients for O&G, however, are quite different and are presumably caused by errors in the COD method, differences in species, product, and perhaps slight differences in the method of extracting. There are, of course, known differences in the lipid composition of these species, especially the C-20 and C-22 polyunsaturated fatty acids. The chain length and configuration of the lipids would have a positive effect on the COD coefficient. For example, some theoretical coefficients are: acetic acid (C_2) 1.066, propionic (C_3) 1.514, myristic (C_{14}) 2.807, melissic (C_{30}) 3.115, lecithin ($C_{44}H_{88}O_9NP$) 2.458, and tristearin ($C_{57}H_{110}O_6$) 2.934. Recognizing the wide variations possible, the empirically derived coefficient of 2.678 seems reasonable.

TABLE 2.—The COD coefficient of several preparations of oil and grease (O&G) and protein from fish and shellfish and from shrimp waste effluent.

Starting material	COD of 1.0 mg/liter of O&G	COD of 1.0 mg/liter of Protein
Black cod, frozen		1.328
Pollock, frozen		1.328
Snow crab, frozen	2.631	
Pink salmon, fresh	2.795	1.326
	2.818	1.345
Pink shrimp, fresh	2.710	1.349
	2.505	1.270
		1.328
Pink shrimp, canned	2.757	1.414
	2.584	1.350
	2.518	
	2.736	
Shrimp waste effluent	2.788	
	2.618	
Mean	2.678	1.338
SD	0.112	0.037

These coefficients are used along with the concentration of protein and O&G to give the COD, i.e., (1.338 mg COD/mg protein)mg protein + (2.678 mg COD/mg O&G)mg O&G = COD_{TR} and assumes that the total COD is the sum of the COD of these two major constituents. To check the validity of this equation the coefficients were multiplied by the predicted values for protein and O&G [obtained from TR_K data and Equations (4) and (5)] and the resulting mean of the sums of the products (2,155 mg COD/liter) was found to be 1.083 times greater than the mean predicted value for COD_{TR} (1,990 mg COD/liter) obtained from TR_K data and Equation (1). Although difficult to prove or demonstrate, we believe that the lower analytical values for COD in a sample of waste effluent are caused by the unequal and competing oxidation of protein and O&G. As is well known, O&G reacts slowly and especially if the dichromate concentration has been reduced from reacting with the more easily oxidized protein. Minor constituents such as nonprotein nitrogen and carbohydrates would contribute to COD in a ratio different from the protein coefficient.Regardless, if the simultaneous equation is to be developed, the inequality must be adjusted by increasing the COD value to equal the sum of the COD of protein plus O&G, i.e.,

$$1.338 \text{ protein} + 2.678 \text{ O\&G} = 1.083 \text{ COD}_{TR}. \quad (6)$$

COD Reaction

The oxidation reaction in the COD method follows the usual chemical reaction laws, i.e., the completeness of the reaction is dependent upon the concentration of the reactants (potassium dichromate and waste). The method uses 25 ml 0.25N or 6.25 meq $K_2Cr_2O_7$ in the reaction flask and 50 ml of effluent. If the effluent is relatively strong, most of the dichromate will be expended in the reaction which results in an incomplete reaction and a lower COD value than if the waste were weak, i.e., having a larger excess of dichromate at the completion of the reaction. Moore and Walker (1956) recommended that the size of sample should be selected so that not more than 50% of the potassium dichromate is used up during the oxidation. To illustrate the relationship between COD and amount of dichromate remaining (the excess) at the end of the 2-h reflux period, data from six protein preparations were combined and plotted in Figure 3. The equation of the regression line was then used to calculate correction factors so that if the COD were determined at an excess dichromate level above or below an arbitrary point of 3.5 meq, the value can be corrected to its value at 3.5 meq. These correction factors are listed in Table 3. To correct COD values, determine the excess dichromate (titration value times normality) and multiply the corresponding factor from Table 2 by the COD determined in the usual way.

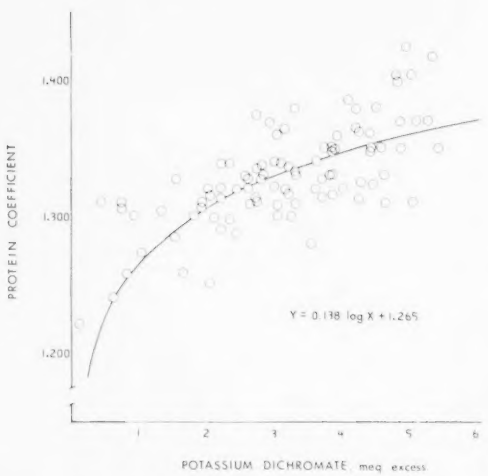

FIGURE 3.—Relationhship between the protein coefficient and the amount of dichromate remaining at the end of the 2-h reflux period.

TABLE 3.—Multiplication factors to correct COD to 3.5 meq dichromate excess.

Excess dichromate (meq)	Multiplication factor	Excess dichromate (meq)	Multiplication factor
2.0	1.026	3.6	0.999
2.1	1.024	3.7	0.998
2.2	1.021	3.8	0.996
2.3	1.019	3.9	0.995
2.4	1.017	4.0	0.994
2.5	1.015	4.1	0.993
2.6	1.014	4.2	0.992
2.7	1.012	4.3	0.991
2.8	1.010	4.4	0.990
2.9	1.009	4.5	0.989
3.0	1.007	4.6	0.988
3.1	1.005	4.7	0.987
3.2	1.004	4.8	0.986
3.3	1.002	4.9	0.985
3.4	1.001	5.0	0.984
3.5	1.000		

Since titration (Jirka and Carter 1975), sample, or reaction errors occur at either end of the curve, we suggest that COD values are valid only between 2 and 5 meq excess. All data for the protein coefficients were determined by obtaining from 10 to 30 COD values at different addition levels (5 to 30 mg protein/50 ml) and plotting the regression line. The coefficient was obtained by substituting the logarithm of 3.5 meq excess into the equation for the regression and solving for COD. In addition, all COD data in Table 1 were corrected to 3.5 meq excess dichromate.

Residue-Ash Correction

The major components of the total residue that contribute to COD are protein and O&G. In addition, various salts and dirt contribute to TR and possibly to COD. Unfortunately, there is no convenient method to measure these minor constituents so we estimate them by determining ash and then subtract to give a corrected value for TR. Since the weight of ash obtained after 500°C drying is less than its corresponding weight when dried at 103°C, the TR_K value (TR − ash) is accordingly greater than it should be. Therefore, the TR_K was reduced as follows: To eliminate variability in individual values, the O&G and protein values were predicted using Equations (4) and (5) for the regression lines in Figure 2 and TR_K data. The sum of the weight of protein plus O&G was found to be about 3% smaller than TR_K, i.e.,

$$\text{protein} + \text{O\&G} = 0.969\ TR_K. \quad (7)$$

This equation corrects the TR_K so that it equals the sum of the protein and O&G, and is convenient to use in this form in the simultaneous equation. The constant, 0.969, is the result of increasing the analytical value for ash by 15.2% and represents, in part, the difference in weight of ash between drying at 500°C and 103°C.

Simultaneous Equation

In the preceding discussion we have shown the two parts of the simultaneous equation: the first showing the sum of the COD from protein and from O&G to be equal to an adjusted total COD, and the second showing the sum of the weights of protein and O&G to be equal to the total residue minus the ash content and corrected for the difference in weight caused by drying at 500°C or 103°C. Equations (6) and (7) are combined in the following so that a simple calculation can serve as a substitute for the difficult direct analyses for protein and O&G:

$$\begin{aligned} X + Y &= 0.969\ TR_K \\ 1.338X + 2.678Y &= 1.083\ COD_{TR} \end{aligned} \quad (8)$$

where: X = protein in milligrams/liter
Y = O&G in milligrams/liter.

This equation should have general application to fishery waste effluents provided: 1) TR_K and COD_{TR} are known or can be derived, and 2) the constant used to increase the value for COD_{TR} has general application. If our assumption is correct that the COD is low because of the incomplete and competitive oxidation of protein and O&G, the constant would apply to any fishery waste having a similar relative amount of protein and O&G, i.e., about 5:1, respectively.

The mean TR and ash data from Table 1 are used to illustrate the use of this equation: From Table 1, TR − ash = 1,431 mg/liter and when substituted into Equation (1) gives a value of 1,990 mg/liter for COD_{TR}. These values, when substituted into the equation and solved for X and Y, give,

$$\begin{aligned} X + Y &= 0.969(1{,}431) \\ 1.338X + 2.678Y &= 1.083(1{,}990) \end{aligned}$$

where: X = 1,163 mg protein/liter
Y = 224 mg O&G/liter.

The calculated values are 29 mg higher for protein and 12 mg lower for oil than the mean analytical values of Table 1 (1,134 and 236, respectively). The differences between data obtained by the direct analysis for protein and O&G and the two methods of calculation are compared in Table 4. A negative or positive sign indicates whether the calculated value is less or more than the analytical value.

The analytical values of sample numbers 1, 2, 3, and 12 for protein and 2 for O&G are obviously in error and although these values were included in the mean values in Table 1, they were omitted from the regression lines and equations of Figure 2. The comparative data indicate that the calculated values are in reasonable agreement with analytical values. Since a regression line determined by the method of least squares is by definition the best fit of empirical data containing normal errors in precision and accuracy, and since protein and O&G are less accurate analyses than TR_K or COD, it follows that a value for O&G calculated from the simultaneous equation or from the equation of the regression line should be more correct than an individually determined value. The data of Equations (4) and (5) in Table 4 are merely a measure of the fit of each value to the regression line. The data of Equation (8), however, are independent of protein and O&G but dependent upon COD and TR data.

If the simultaneous equation is used to calculate O&G, TR_K and COD_{TR} are required for the equation and can be obtained through analysis and calculation, respectively. Alternatively, O&G or

TABLE 4.—Comparison by difference of protein and O&G data obtained by analysis or by calculation.

Sample no.	Protein mg/liter			O&G mg/liter		
	Analysis	Eq. (4)	Eq. (8)	Analysis	Eq. (5)	Eq. (8)
1	831	+98	+104	185	−24	−39
2	1,319	+266	+265	486	−147	−129
3	1,215	+107	+206	276	−9	−101
4	1,281	−2	+33	258	−2	−32
5	1,056	+13	−1	203	−4	+8
6	1,075	+34	+9	230	−20	+4
7	1,212	+8	+63	229	+11	−42
8	1,037	−8	−44	195	−7	+25
9	1,425	−20	−24	302	−12	+2
10	1,175	−15	+1	204	+20	+5
11	1,025	−24	−22	186	−5	−13
12	1,116	−61	−102	175	+20	+59
13	1,188	+3	+9	233	−1	−6
14	925	−12	−35	148	+9	+23

protein can be calculated from the regression of O&G and protein on TR_K. For practical reasons, we prefer using the simultaneous equation because establishing the base data would be difficult at the plant level in that both protein and O&G should be determined and correlated with COD and TR_K to establish the accuracy of the analyst.

Occasionally, wild values might occur in analyses but the average of the standard deviations between duplicate analyses for TR_K, FR_K, COD_{TR}, and COD_{FR} in this paper was 6.1, 3.6, 14.4, and 10.1 mg/liter, respectively. Using the 6 mg/liter TR_K figure the predicted value for COD from 1,431 ± 12 mg TR_K is 1,990 ± 17 mg COD from Equation (1). Based on this interval of two standard deviations, protein and O&G values obtained by the simultaneous equation could vary as follows:

TR_K	COD_{TR}	Protein	O&G
1,419	1,973	1,153	222
1,431	1,990	1,163	224
1,443	2,007	1,172	226

RECOMMENDATION

We recommend that this simplified testing-calculating system be used by the fishing industry provided proper regulatory approval is obtained. The following background data will be required:

1. Determine the regression of COD_{TR} and COD_{FR} on TR_K and FR_K and calculate the equations [i.e., Equations (1), (2), (3)]. Use grab samples (about 10) to give a good spread of data.
2. For protein and O&G, either a regression or a simultaneous equation can be used.
   (A) Obtain O&G and protein data on the same samples as above and determine the equation of the regressions of protein and O&G on TR_K [i.e., Equations (4) and (5)].
   (B) Determine the ratio or weight of protein to weight of O&G on several samples and if between 4.6 and 5.9, the constant (1.083) in Equation (8) is assumed valid. If not, the constant must be recalculated in order that the COD_{TR} equals the sum of COD from protein and O&G [see discussion for Equation (6)].
   (C) The O&G coefficient should be determined on fishery waste effluents in which the oil may give a significantly different value than 2.678.

The routine application of this system would be as follows:

1. Determine COD_{FR}, TR, and ash by direct analysis.
2. Subtract ash from TR to give TR_K.
3. Substitute into Equations (1) and (2) and solve for COD_{TR} and FR_K.
4. Obtain COD_{NFR} and NFR_K by difference or by Equation (3).
5. Obtain protein and O&G from Equations (4), (5), or (8).

Thus, three simple and accurate tests give reportable data on nine parameters which more completely describe the pollutant load released to the environment than those currently in use.

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AMERICAN SOLENOCERID SHRIMPS OF THE GENERA *HYMENOPENAEUS, HALIPOROIDES, PLEOTICUS, HADROPENAEUS* NEW GENUS, AND *MESOPENAEUS* NEW GENUS

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

Twelve American species, one from Hawaii, are assigned to five genera: five to *Hymenopenaeus*, one to *Haliporoides*, two to *Pleoticus*, three to *Hadropenaeus*, and one to *Mesopenaeus;* the latter two genera are described herein. Each of the genera is defined and the relationships among them are discussed. The species are described in detail mostly on the bases of collections made in the western Atlantic and eastern Pacific during cruises of 29 exploratory vessels. For each species a diagnosis, illustrations, references, disposition of types, locality records, and geographic as well as bathymetric ranges are provided. The affinities of each species are indicated, and variations of several morphological and morphometric characters are analyzed. Keys for the identification of all taxa are given. Photophores were discovered in *Hadropenaeus affinis*, here recognized as a distinct species, and *Mesopenaeus tropicalis*. The spermatophores of three, *Pleoticus robustus, P. muelleri*, and *M. tropicalis* (those of the latter previously unknown), are described and their mode of attachment to the females is discussed. The range of *Hymenopenaeus debilis* was found to extend south of the Gulf of Mexico, through the Caribbean to Guyana, and that of *H. aphoticus* to include the Caribbean. *Pleoticus muelleri* is now known to occur north of the state of Rio de Janeiro, off Espírito Santo, and *Hadropenaeus affinis* is newly reported from the southeast Atlantic coast of the United States, where it ranges as far north as Cape Lookout, N.C.

This work is part of a continuing study of the systematics and distribution of the American members of the superfamily Penaeoidea. Extensive collections made during cruises of 26 exploratory vessels provided excellent series of specimens from the western Atlantic. In contrast, the material available from the tropical and subtropical eastern Pacific (including that obtained during cruises of three exploratory vessels) is rather meager and these waters still remain appallingly unexplored, particularly beyond the 100-m contour. Few benthic collections from the latter region have been deposited in American institutions since the expeditions of the *Albatross* in 1889 and 1891. The only major ones are those resulting from the explorations sponsored by the Allan Hancock Foundation and Scripps Institution of Oceanography among which no member of the genera investigated in the present project has been found.

The only species treated here from waters not adjacent to the American continent is one which ranges throughout the Indo-West Pacific, reaching Hawaii. This shrimp is included because it is the third member of a new genus, the other two being found off American shores. Inasmuch as the Hawaiian population of the species has not been adequately described and because numerous specimens from the area are available to me, a detailed account of its morphology is presented.

The five genera treated in this paper, together with *Solenocera* and *Haliporus*, constitute the family Solenoceridae, a group that has been previously considered one of the four subfamilies of Penaeidae. I am of the opinion that because of the basic differences among these four suprageneric groups they should be elevated to the category of families, i.e., Aristeidae, Solenoceridae, Penaeidae, and Sicyoniidae, as has been defended by Pérez Farfante (in press). The western Atlantic species of *Solenocera* (the other genus of Solenoceridae which is present in the region, in addition to four of those discussed here) were recently monographed by Pérez Farfante and Bullis (1973).

In the diagnoses of the genera and descriptions of the 12 species discussed here, many morphological characters have been studied in order to base relationships at generic and specific levels.

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560.

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For each taxon a synonymy, bibliographic references (selected for the genera, and complete for the species), location of type-specimens, descriptions, and distributional data are given, as are variations for some species. Detailed accounts of the spermatophores (both as attached to the females and as they appear when removed from the terminal ampullae of the males) of three species are also presented. These are the only species for which spermatophore-bearing females were secured.

Bate (1881) was the first to describe species of the generic complex treated here, assigning all except one—which was assigned to *Solenocera* Lucas (1849)—in a new genus, *Haliporus*. A year later, Smith (1882) proposed the genus *Hymenopenaeus* for another new species belonging to that complex. Subsequently, Bate (1888) expanded his preliminary descriptions of *Haliporus* and corresponding species, and pointed out that the one he had placed in *Solenocera,* together with two others, should be relegated to a new genus, *Philonicus*. After his manuscript was in press, he discovered that the latter name was preoccupied and changed it to *Pleoticus* in the Introduction. Bouvier (1906b) presented a revision of the genus *Haliporus* in which he recognized 19 species, most of which had been described after Bate's last contribution (1888). He separated them into three groups on the basis of the relative length of the posterior two pairs of pereopods, the relative diameter of the proximal part of the respective carpi, and the consistency of the integument. He failed to recognize other important supraspecific differences which led him to group together species which are not closely related. Burkenroad (1936) disagreed with Bouvier's arrangement and, as a result of an extensive investigation, recognized two genera, *Haliporus* and *Hymenopenaeus*. Several other generic names have been proposed and later synonymized with *Hymenopenaeus,* a clear indication of the taxonomic difficulties presented by this complex.

The genus *Hymenopenaeus* was defined by Burkenroad (1936) as those "Solenocerinae without podobranchs behind VIII; with well-developed prosartema and only a single pair of lateral telson spines in adult stages, and with cylindrical filiform antennular flagella." Within it, he recognized four separate groups based on the presence or absence of branchiostegal or pterygostomian spines and the arrangement of the epigastric and rostral teeth.

An examination of Atlantic, eastern Pacific, and Hawaiian species, supplemented by material from the Indo-West Pacific region, convinces me that, in addition to the arrangement of the middorsal teeth on the carapace, the following characters are more reliable than the branchiostegal and pterygostomian spines in ascertaining interrelationships of the species previously included in *Hymenopenaeus:* shape of the antennular flagella and rostrum, proportions of the carapace, number and comparative size of the articles of the mandibular palp, presence or absence of certain carinae on the carapace, relative dimensions of the posterior two pairs of pereopods, location of the distolateral spine (terminal or subterminal) of the lateral ramus of the uropod, structure of the petasma, and degree of development of the arthrobranchia on somite VII.

A comparative study based on the characters cited above indicates that the species under consideration should be assigned to five genera: *Hymenopenaeus, Pleoticus,* and *Haliporoides*—which had been erected previously—and *Hadropenaeus* and *Mesopenaeus*—which are proposed here.

Diagnoses of the four groups established by Burkenroad (1936) within *Hymenopenaeus* together with the conclusions resulting from my revision of this species-complex follow.

Group I. This division contained the western Atlantic *H. muelleri* and *H. tropicalis,* and the Indo-West Pacific (Red Sea) *H. steindachneri*. As pointed out by Burkenroad, these species share the arrangement of the epigastric and rostral teeth, which are separated by regularly decreasing intervals anteriorly, and the absence of branchiostegal and pterygostomian spines; to these characters may be added the presence of orbital spines and the lack of distinct branchiocardiac carinae. Several different features occur in *tropicalis* which I consider to be of sufficient importance to justify a separate genus, for which I propose the name *Mesopenaeus*. Moreover, the western Atlantic *robustus,* which was placed in Group II by Burkenroad, shares basic characters with *muelleri* and *steindachneri;* consequently, the three are grouped herein under the available generic name *Pleoticus* Bate (1888).

Group II. The species assigned to this group were characterized by possessing branchiostegal but lacking pterygostomian spines and, like those of Group I, exhibit epigastric and rostral teeth separated by regularly decreasing intervals.

Burkenroad subdivided the group into two sections: section 1, with orbital spines, to which only *H. robustus* was assigned, and section 2, without orbital spines, to which the western Atlantic *H. modestus* and the Indo-West Pacific *H. lucasii* were referred. As stated above, the former species is here transferred to the genus *Pleoticus,* and the latter two, together with the amphi-Atlantic *H. affinis* (which Burkenroad considered as "very doubtfully distinct" from *H. modestus*), are placed in the genus *Hadropenaeus.*

Group III. This group comprised the species with pterygostomian but lacking branchiostegal spines, and with the epigastric tooth separated from the rostral teeth by a long interval. The eastern Pacific *H. diomedeae* and the Indo-West Pacific *H. sibogae* and *H. triarthrus* were included, but these three species are referred here to the genus *Haliporoides* Stebbing 1914.

Group IV. This assemblage contained those species that are armed with branchiostegal spines, and have the epigastric and first rostral teeth separated from the remaining rostral teeth by a conspicuous interval. It was subdivided into two sections characterized by the presence or absence of pterygostomian spines. In section 1, Burkenroad cited *Hymenopenaeus laevis,* found on both sides of the Atlantic and in the Indo-West Pacific, and *H. doris* and *H. nereus* of the American Pacific; in section 2, he included the Atlantic *H. aphoticus* and *H. debilis* and the Indo-West Pacific *H. aequalis, H. obliquirostris, H. neptunus,* and *H. propinquus.* Since the publication of Burkenroad's work, one species, the Indo-West Pacific *H. sewelli,* has been added to section 1, and three have been added to section 2: one from the eastern Atlantic, *H. chacei,* and two from the Indo-West Pacific, *H. fattahi,* and *H. halli.* These species are included in *Hymenopenaeus* as restricted here, and their separation into two sections is recognized.

Burkenroad also discussed under *Hymenopenaeus* the two following Indo-West Pacific species: *Haliporus villosus* Alcock and Anderson 1894 (syntype illustrated in Alcock and Anderson 1896), and *Haliporus taprobanensis* Alcock and Anderson 1899 (holotype illustrated in Alcock 1899b). He indicated that the former perhaps would merit being placed in an independent group, and pointed out that although the latter shares several characters with members of Group III, it differs from them in other basic features. Our knowledge of *H. villosus* prior to Kensley's (1968) study was limited to the brief description by Alcock and Anderson (1894) and their illustration published in 1896 (plate 26, figure 1). The lack of detail in the figure of the telson, exhibiting no movable spines, was probably responsible for Burkenroad's assigning this shrimp to the genus *Hymenopenaeus.* Kensley presented a detailed description and several illustrations which demonstrate that this species exhibits two basic features characteristic of the genus *Haliporus* (as restricted by Burkenroad 1936): in addition to the podobranchia on the second maxilliped, another, small one is present on the third maxilliped, and the telson is armed with movable spines situated anterior to the fixed pair. My examination of two specimens of *H. taprobanensis* has shown that the same characters are present in them; thus, in respect to these two features, both this species and *H. villosus* are more closely allied to the members of *Haliporus* than to those assigned to *Hymenopenaeus.* It should be pointed out, however, that *H. villosus* and *H. taprobanensis* differ from *Haliporus curvirostris* Bate 1881, the type-species, in several characters (e.g., shape of rostrum, number of podobranchiae posterior to the second maxilliped, carinae present on the carapace) which seem to me to be of supraspecific significance. Consequently, I believe that a study of adequate material might demonstrate that they should be relegated to separate monotypic genera.

Although the illustration of the entire animal of *H. villosus* by Alcock and Anderson (1896) and that by Kensley (1968) leave little doubt that both correspond to the same species, the specimens available to the former authors were densely covered by setae, as they explicitly stated, whereas that studied by Kensley as well as the specimens examined by me are glabrous. The material available to Alcock and Anderson was from the Laccadive Sea, off southwest India; Kensley's specimen was caught off southwest of South Africa, and the two at my disposal were collected off eastern Madagascar.

All five genera (together with *Haliporus* and *Solenocera*) are believed to have arisen from a common solenoceroid ancestor, some of the characters of which are presented in the accompanying dendrogram. In the latter only the newly acquired characters or those modified or lost in each lineage are indicated. As shown in the dendrogram, one of the lines arising from the solenoceroid ancestor led to *Haliporus,* apparently not only the most primitive solenocerid, but

CHARACTERISTICS INVOLVED IN THE EVOLUTION OF SOLENOCERIDAE
(See text for explanation)

Solenocera
Antennular flagella strongly flattened, ventral pair forming trough, four together constituting respiratory siphon
Petasma with dorsolateral lobule bearing terminal process
Lateral ramus of uropod lacking distolateral spine
Mesopenaeus
Antennular flagella dissimilar, dorsal subcylindrical, ventral depressed
Fourth and fifth pereopods stout proximally, fifth moderately longer than fourth
Petasma with ventral costa fused to flexible terminal part of ventrolateral lobule
Hadropenaeus
Antennular flagella usually subcylindrical, occasionally ventral one depressed
Fifth pereopod flagelliform and considerably longer than fourth
Petasma with ventral costa free from heavily sclerotized terminal part of ventrolateral lobule
Carapace proportionately short
Rostrum deep, with ventral margin convex
Submarginal carina absent
Pleoticus
Submarginal carina sharp
Petasma with ventral costa free from flexible terminal part of ventrolateral lobule
Haliporoides
Integument firm
Epigastric tooth separated from rostral teeth
Posthepatic carina absent
Fourth and fifth pereopods relatively stout proximally, moderately long
Hymenopenaeus
Integument thin, flexible
Epigastric and first rostral teeth widely separated from remaining rostral teeth
Posthepatic carina present
Fourth and fifth pereopods flagelliform, very long
Branchiocardiac carina lacking
Fourth and fifth pereopods rather stout proximally, fifth moderately longer than fourth
Petasma with distal part of ventral costa fused to adjacent flexible portion of ventrolateral lobule
Telson with single pair of fixed lateral spines only
Podobranchia on second maxilliped only
Haliporus
Telson with pairs of movable spines anterior to fixed pair
Podobranchia on at least second and third maxillipeds
Solenoceroid ancestor
Carapace elongate
Rostrum low
Epigastric and rostral teeth separated by intervals regularly decreasing anteriorly
Postorbital spine present
Branchiocardiac and submarginal carinae present
Lateral ramus of uropod bearing distolateral spine
Antennular flagella similar, subcylindrical
Podobranchiae on appendages posterior to second maxilliped
Petasma lacking terminal process

according to Burkenroad (1963b) "the Recent Peneid which seems in several respects the nearest of these to the stem-form of the relatively primitive suborder Dendrobranchiata." A second line gave rise to *Hymenopenaeus* and *Haliporoides,* and a third lineage is believed to have been ancestral to two stocks, one of which terminated in *Pleoticus* and from the other evolved *Hadropenaeus, Mesopenaeus,* and *Solenocera;* the latter appears to be the most specialized of all seven genera.

The members of Solenoceridae, in general, occupy deep water beyond the continental and insular shelves; however, most of the species of *Solenocera* as well as *Pleoticus muelleri* are restricted to shallow water. *Mesopenaeus tropicalis*

is found both on the shelves, at a minimum depth of 30 m, and on the slopes to about 500 m.

Material

Abbreviations of the repositories of the specimens examined during this study follow:

AMNH	American Museum of Natural History, New York, N.Y.
BMNH	British Museum (Natural History), London.
IOUSP	Instituto Oceanográfico, Universidad de São Paulo, São Paulo.
MCIP	Ministerio de Comercio e Industrias, Panama.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MP	Muséum National d'Histoire Naturelle, Paris.
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands.
TAMU	Texas A&M University, College Station, Tex.
UMML	Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Fla.
UNC-IMS	University of North Carolina - Institute of Marine Sciences, Morehead City, N.C.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.

Presentation of Data

The measurement of carapace length (cl) is the linear distance between the orbital margin and the midposterior margin of the carapace, and that of total length (tl) is the distance between the apex of the rostrum and the posterior end of the telson. The scales accompanying the illustrations are in millimeters. Figures 1 and 2 depict many characters used in the descriptions. For the terminology employed in the accounts of the spermatophores, see Pérez Farfante (1975).

Key to Genera of Solenoceridae

1. Telson with pairs of movable lateral spines anterior to fixed pair; podobranchia on at least second and third maxillipeds ..... *Haliporus*
   Telson with single pair of fixed lateral spines only; podobranchia restricted to second maxilliped 2

2. Dorsal and ventral antennular flagella lamellate; lateral ramus of uropod lacking distolateral spine ..... *Solenocera*
   Dorsal antennular flagellum subcylindrical, ventral subcylindrical or flattened; lateral ramus of uropod armed with distolateral spine 3

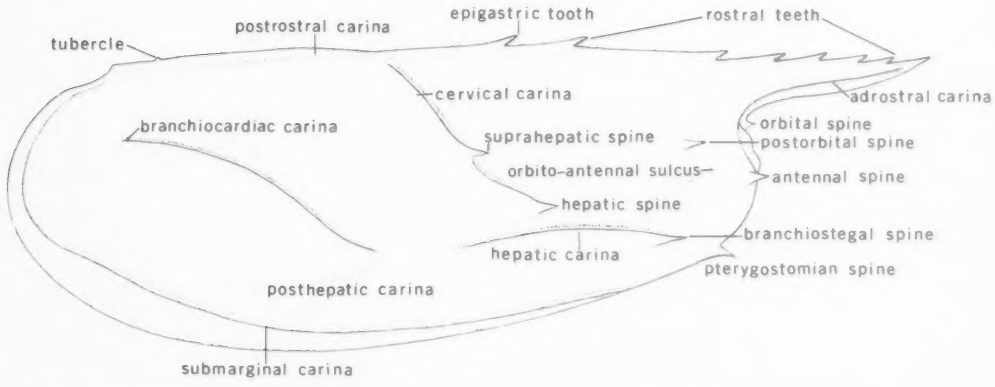

FIGURE 1.—Diagrammatic lateral view of cephalothorax showing terms used in descriptions of solenocerid shrimps.

3. Ventral antennular flagellum conspicuously depressed, orbital spine present ..... *Mesopenaeus*
   Ventral antennular flagellum subcylindrical, occasionally depressed, if so orbital spine lacking 4

4. Epigastric tooth separated from first rostral by interval not conspicuously smaller or greater than that between first and second rostral teeth 5
   Epigastric or epigastric and first rostral teeth separated from remaining teeth by relatively long interval 6

5. Rostrum low, with ventral margin straight or concave; submarginal carina present ..... *Pleoticus*
   Rostrum deep, with ventral margin pronouncedly convex; submarginal carina absent ..... *Hadropenaeus*

6. Epigastric and first rostral teeth separated from remaining ones by long interval; suprahepatic spine absent .... *Hymenopenaeus*
   Epigastric tooth separated from rostral teeth by long interval; suprahepatic spine present ..... *Haliporoides*

Hymenopenaeus Smith 1882

Haliporus Bate 1881:185 [part, excluding *Haliporus curvirostris* Bate 1881]. Bate 1888:284 [part]. Faxon 1893:213 [part]; 1895:189 [part]. Alcock 1901:22 [part]. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part]. Fowler 1912:542 [part].

Hymenopenaeus Smith 1882:91 [type-species by monotypy, *Hymenopenaeus debilis* Smith 1882. Gender, masculine. Placed on the Official List of Generic Names in Zoology as Name No. 1816, International Commission on Zoological Nomenclature (1969), Opinion 864]. Smith 1885: 179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part]. Holthuis 1962:108. International Commission on Zoological Nomenclature 1969:139. Roberts and Pequegnat 1970: 29 [part].

Diagnosis.–Body slender, carapace elongate, integument thin, flexible. Rostrum variable in length, reaching between distal 0.25 of first antennular article and end of peduncle; ventral margin straight; usually armed only with dorsal teeth, occasionally also with ventral teeth; epigastric and first rostral teeth separated from remaining teeth by relatively long interval. Orbital spine absent; postorbital, antennal, hepatic, and branchiostegal spines present; pterygostomian spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; branchiocardiac carina sharp, accompanying sulcus deep; posthepatic and submarginal carinae present. Abdomen carinate dorsally at least along posterior three somites. Prosartema moderately long, flexible. Telson with pair of conspicuous fixed, lateral spines. Antennular flagella similar, filiform, and longer than carapace. Mandibular palp two-jointed, articles relatively narrow, distal one much shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis), gently narrowing to rounded apex. Fourth and fifth pereopods extremely long and flagelliform. First pereopod with spine on

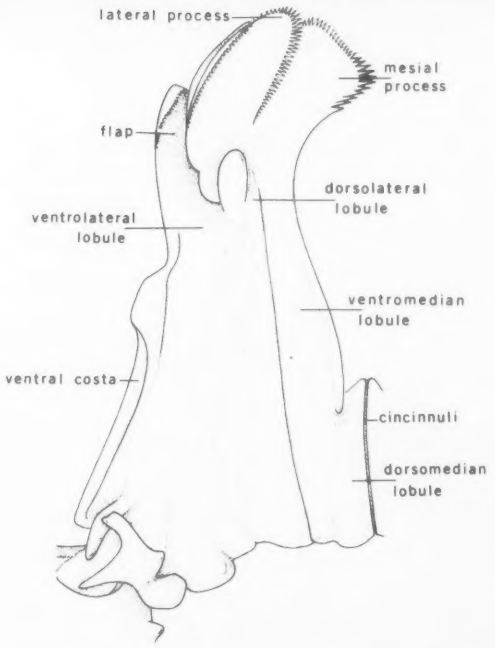

FIGURE 2.—Left half of petasma (dorsal view) of *Hymenopenaeus debilis* showing terms used in descriptions.

basis and usually on ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine, reaching distal margin of lamella (terminal spine). In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal end of rib of dorsolateral lobule elevated above adjacent area and not projecting beyond distal margin; ventromedian lobule usually produced in conspicuous processes distally; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate, ventrolateral ("posterior") spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; rudimentary arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Following are the species listed in each of the two sections proposed by Burkenroad (1936), a division with which I am in full agreement.

Section 1. Pterygostomian spine present.
Atlantic, Indo-West Pacific: *Hymenopenaeus laevis* (Bate 1881). Indo-West Pacific: *Hymenopenaeus sewelli* Ramadan 1938. Eastern Pacific: *Hymenopenaeus doris* (Faxon 1893); *Hymenopenaeus nereus* (Faxon 1893).

Section 2. Pterygostomian spine absent.
Atlantic: *Hymenopenaeus aphoticus* Burkenroad 1936; *Hymenopenaeus debilis* Smith 1882; *Hymenopenaeus chacei* Crosnier and Forest 1969. Indo-West Pacific: *Hymenopenaeus aequalis* (Bate 1881); *Hymenopenaeus fattahi* Ramadan 1938; *Hymenopenaeus halli* Bruce 1966; *Hymenopenaeus neptunus* (Bate 1888); *Hymenopenaeus obliquirostris* (Bate 1881); *Hymenopenaeus propinquus* (de Man 1907).

Affinities.–The members of the genus *Hymenopenaeus* differ from those of the closely related *Haliporoides, Pleoticus, Hadropenaeus* n. gen., and *Mesopenaeus* n. gen., in having a more slender body; a thin, flexible, almost membranous integument; the epigastric and first rostral teeth separated from the remaining teeth by an interval longer than the spaces between the more anterior teeth; and in possessing a posthepatic carina. They also differ from those of the other genera in having a slender mandibular palp in which the distal article is much shorter than the basal; extremely long and flagelliform fourth and fifth pairs of pereopods, and in certain features of the petasma: the terminal part of the ventrolateral lobule forms a flap to which the ventral costa is fused, the rib of the dorsolateral lobule is elevated distally from the surrounding area, and the ventromedian lobule is produced distally into conspicuous processes.

Remarks.–In the widely utilized work of Kubo (1949) several statements are made which should be discussed. Kubo based his description of the genus *Hymenopenaeus* primarily on two species found in Japanese waters [*H. lucasii* (Bate 1881) and *H. aequalis* (Bate 1888)], which led him to make erroneous generalizations. First, he considered the presence of two, instead of one, arthrobranchiae on somite VII as a character typical of *Solenocera,* and in his key to the genera of the subfamily Solenocerinae utilized this character to distinguish it from other genera in the subfamily. In at least one species (*Pleoticus robustus,* previously included in *Hymenopenaeus*), of a genus other than *Solenocera,* however, I find that there are two arthrobranchiae on somite VII. Secondly, Kubo noted that the petasma in *"Hymenopenaeus"* possessed spinules along the distal margin; actually, in some species they are absent. Finally, in the section "Arrangement of branchiae" Kubo indicated the restriction of podobranchia to somite VIII (on second maxilliped) in the members of the subfamily Solenocerinae, and in his table 6D he noted the presence of only one podobranchia in *Hymenopenaeus* and *Parahaliporus* (=*Haliporoides*). In the key to the genera of the subfamily, however, he utilized the occurrence of a rudimentary podobranchia on somites IX and X as the only feature to distinguish *Hymenopenaeus* from *Haliporus* and *Parahaliporus.* He used this feature in the key although in the following description of the genus *Hymenopenaeus,* he stated that in the specimens of *H. lucasii* and *H. aequalis* at his disposal, the epipods of none of the thoracic appendages behind the second maxilliped are furnished with podobranchia. It thus seems that in the key the line corresponding to *Hymenopenaeus* and the line corresponding to *Parahaliporus* and *Haliporus* were transposed; however, podobranchiae are present behind somite VIII in *Haliporus*

(at least on the third maxilliped and as far as the third pereopod) but not in *Parahaliporus*.

Key to Species of *Hymenopenaeus* in American Waters

1. Pterygostomian spine present (section 1) ..2
   Pterygostomian spine absent (section 2) ...4

2. Scaphocerite, at most, barely overreaching antennular peduncle. Rostrum, in adult, falling short of distal end of first article of antennular peduncle. Females with pyramidal, median protuberance on sternite XIV projecting ventrally. Males with ventromedian lobule of petasma bearing two or three small triangular processes distomesially .... *H. laevis*
   Scaphocerite overreaching antennular peduncle by, at least, 0.25 of its own length. Rostrum, in adult, surpassing distal end of first antennular article 3

3. Females lacking median protuberance on sternite XIV. Males with petasma bearing subrectangular distomesial process projecting at right angle to mesial margin, and armed with long spines ..... *H. nereus*
   Females with subpyramidal median protuberance on sternite XIV projecting anteroventrally. Males unknown . *H. doris*

4. Eye with cornea hemispherical and disposed such that imaginary line extending from mesial tubercle parallel to basal margin of ocular peduncle intersects lateral border of latter far proximal to proximolateral extremity of cornea ..... *H. aphoticus*
   Eye with cornea subreniform and disposed such that line extending from mesial tubercle parallel to basal margin of ocular peduncle intersects posterolateral extremity of cornea ..... *H. debilis*

Hymenopenaeus debilis Smith 1882

Figures 2, 3, 4B, 5-9

Hymenopenaeus debilis Smith 1882:91, pl. 15, fig. 6-11, pl. 16, fig. 1-3 [syntypes: 1 ♀, SE of Savannah Beach, Ga., 31°57′00″N, 78°18′35″W, 333 fm (609 m), 12 July 1880, *Blake* stn 317. 1 ♀, MCZ 3270, SE of Cape Fear, N.C., 33°19′00″N, 76°12′30″W, 457 fm (836 m), 14 July 1880, *Blake* stn 323. 1 ♀, USNM 4920, E of Cape Fear, N.C., 33°42′15″N, 76°00′50″W, 464 fm (849 m), 14 July 1880, *Blake* stn 326]. Smith 1887:687, pl. 16, fig. 7. Burkenroad 1936:111, fig. 63-64. Yokoya 1941:52. Anderson and Lindner 1945: 289. Harvey 1952:352. Ramadan 1952:9, fig. 22-23. Springer and Bullis 1956:7. Holthuis 1962: 108. Boschi 1964:38. Bullis and Thompson 1965:5. Zariquiey Alvarez 1968:47, fig. 24b. Crosnier and Forest 1969:545. International Commission on Zoological Nomenclature 1969: 139. Roberts and Pequegnat 1970:31. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:269, fig. 85 c-d, 87b, 89a.

Haliporus debilis. Faxon 1896:163. Bouvier 1905a:980; 1906a:253; 1906b:3; 1908:83, pl. 1, fig. 6, pl. 14, fig. 9-18. A. Milne Edwards and Bouvier 1909:206, pl. 2, fig. 8. de Man 1911:7. Fowler 1912:543. Boone 1927:78. Maurin 1961: 530; 1968:484. Vilela 1970:122.

Haliporus debilis var. *africanus* Bouvier 1908:83 [syntypes: 4 ♂ 3 ♀, MP, off Mazaghan, 33°46′N, 9°02′W, 1,319 m, 14 June 1883, *Talisman* stn 21].

Material

UNITED STATES—New Jersey: 1 ♀, USNM, Hudson Canyon, 550-600 m, 17 August 1972, *Gosnold* stn 123. 1 ♂, USNM, off Barnegat Inlet, 768 m, 3 August 1884, *Albatross* stn 2187. 1 ♂, USNM, N of Little Egg Inlet, 984 m, 19 August 1884, *Albatross* stn 2201. North Carolina: 6 ♂ 6 ♀, UNC-IMS, E of Cape Fear, 495-490 m, 29 July 1970, *Eastward* 19 stn 14954. 1 ♀ syntype, USNM 4920, E of Cape Fear, 849 m, 14 July 1880, *Blake* stn 326. 1 ♀ syntype, MCZ 3270, SE of Cape Fear, 836 m, 14 July 1880, *Blake* stn 323. 5 ♂ 4 ♀, USNM, SE of Cape Fear, 744 m, 6 May 1886, *Albatross* stn 2676. Georgia: 1 ♀, USNM, off St Catherines I, 814 m, 25 June 1961, *Atlantis* stn A-266-2. Florida: 4 ♀, USNM, NE of Cape Kennedy, 922 m, 3 May 1886, *Albatross* stn 2660. 6 ♂, USNM, NE of Cape Kennedy, 931 m, 3 May 1886, *Albatross* stn 2659. 3 ♀, USNM, SE of Key West, 558-514 m, 29 August 1967, *Gerda* stn 861. 1 ♀, USNM, off St Petersburg, 465 m, 29 September 1951, *Oregon* stn 489. 1 ♀, USNM, off Destin, 512 m, 14 March 1885, *Albatross* stn 2397. 1 ♂ 1 ♀, TAMU, off Santa Rosa I, 565 m, 4 August 1968, *Alaminos* stn 68A7-10A. 1 ♀, TAMU, off Gulf Beach, 1,061 m, 7 August 1968, *Alaminos* stn 68A7-13A. Alabama: 2 ♀, USNM, off Orange Beach, 585 m, 13 August 1970, *Oregon II* stn 11146. 1 ♂ 5 ♀, USNM, S of Mobile Bay, 366 m, 18 December 1962, *Oregon* stn 4151. Louisiana: 1 ♂ 1 ♀, USNM, E of Mississippi Delta, 439-448 m, 17 July 1960, *Oregon* stn 2825. 1 ♀, USNM, E of Southeast Pass, Mississippi Delta, 626 m, 11 February 1885, *Albatross* stn 2376. 3 ♀, TAMU, off Garden I Bay, Mis-

sissippi Delta, 476 m, 15 October 1969, *Alaminos* stn 69A13-40. 1 ♂ 7 ♀, USNM, E of Mississippi Delta, 457 m, 10 June 1959, *Silver Bay* stn 1203. 1 ♂ 1 ♀, MCZ, SE of Mississippi Delta, 587 m, 1878, *Blake* stn 47. 28 ♂ 121 ♀ 110 juv and larvae, YPM, S of Grand Terre Is, 302 m, 26 March 1936, *Atlantis* stn 2381. 1 ♀, YPM, S of Grand Isle, 356 m [in *Atlantis* log 300 fm, 549 m], 23 March 1937, *Atlantis* stn 2831. 6 ♂ 11 ♀, USNM, SW of Ship Shoal Lighthouse, 549 m, 23 February 1964, *Oregon* stn 4709. Texas: 1 ♀, TAMU, off Port Aransas, 476 m, 19-20 November 1968, *Alaminos* stn 68A13-22. 2 ♀, USNM, off Padre I, 585-658 m, 20 July-6 August 1969, *Western Gulf* stn 35. 1 ♀, USNM, off Padre I, 501 m, 21 March 1969, *Oregon II* stn 10456.

MEXICO—Tamaulipas: 1 ♀, TAMU, SW of Matamoros, 713 m [according to label], 12 November 1968, *Alaminos* stn 68A13-3. 1 ♀, TAMU, SW of Matamoros, 878 m, 12 November 1968, *Alaminos* stn 68A13-1. Quintana Roo: 2 ♀, USNM, off Cabo Catoche, 585 m, 13 August 1970, *Oregon II* stn 11146.

BAHAMA ISLANDS—1 ♀, RMNH, NW of Matanilla Reef, 662-702 m, 18 July 1965, *Gerda* stn 671. 2 ♂ 5 ♀, RMNH, NW of Great Stirrup Cay, 733-897 m, 4 July 1963, *Gerda* stn 190. 1 ♂, USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, *Gerda* stn 815.

GREATER ANTILLES—1 ♂ 4 ♀, USNM, N of Puerto Rico, 732-658 m, 30 January 1933, Johnson-Smithsonian Deep-Sea Exp., stn 1. 1 ♀, USNM, N of Puerto Rico, 476 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 23. 1 ♂, USNM, N of Puerto Rico, 512 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 24. 1 ♀, RMNH, SW of Navassa I, Jamaica Channel, 1,034 m, 2 July 1970, *Pillsbury* stn 1187.

LESSER ANTILLES—1 ♂ 5 ♀, USNM, SW of Sombrero I, 664-704 m, 23 July 1969, *Pillsbury* stn 989. 1 ♂ 2 ♀, USNM, off Dog I, 688 m, 6 December 1969, *Oregon II* stn 10834. 1 ♀, USNM, W of Dog I, 658 m, 10 December 1969, *Oregon II* stn 10847. 5 ♀, USNM, W of Saba Bank, 786 m, 3 December 1969, *Oregon II* stn 10833. 1 ♂ 3 ♀, USNM, E of Standfast Pt, Antigua, 786-1,125 m, 18 July 1969, *Pillsbury* stn 954. 2 ♀, USNM, Guadeloupe Passage, 738-832 m, 17 July 1969, *Pillsbury* stn 946. 1 ♀, USNM, off Point du Nord, Marie Galante I, 704-732 m, 12 July 1969, *Pillsbury* stn 919. 3 ♂ 14 ♀, USNM, E of Capesterre, Guadeloupe I, 549-686 m, 14 July 1969, *Pillsbury* stn 923. 8 ♀, USNM, off Dominica I, 808 m, 5 March 1966, *Oregon* stn 5930. 2 ♀, USNM, off Dominica I, 607 m, 4 March 1966, *Oregon* stn 5927. 2 ♂ 3 ♀, USNM, off Vieux Fort, St Lucia, 417-589 m, 9 July 1969, *Pillsbury* stn 904. 2 ♂, USNM, NE of Soufrière, St Vincent, 576-842 m, 6 July 1969, *Pillsbury* stn 881.

BELIZE—2 ♂ 4 ♀, YPM, N of Glover Reef, 885 m, 20 March 1925, *Pawnee*.

NICARAGUA—5 ♀, USNM, off Punta de Perlas, 613 m, 22 November 1968, *Oregon II* stn 10207.

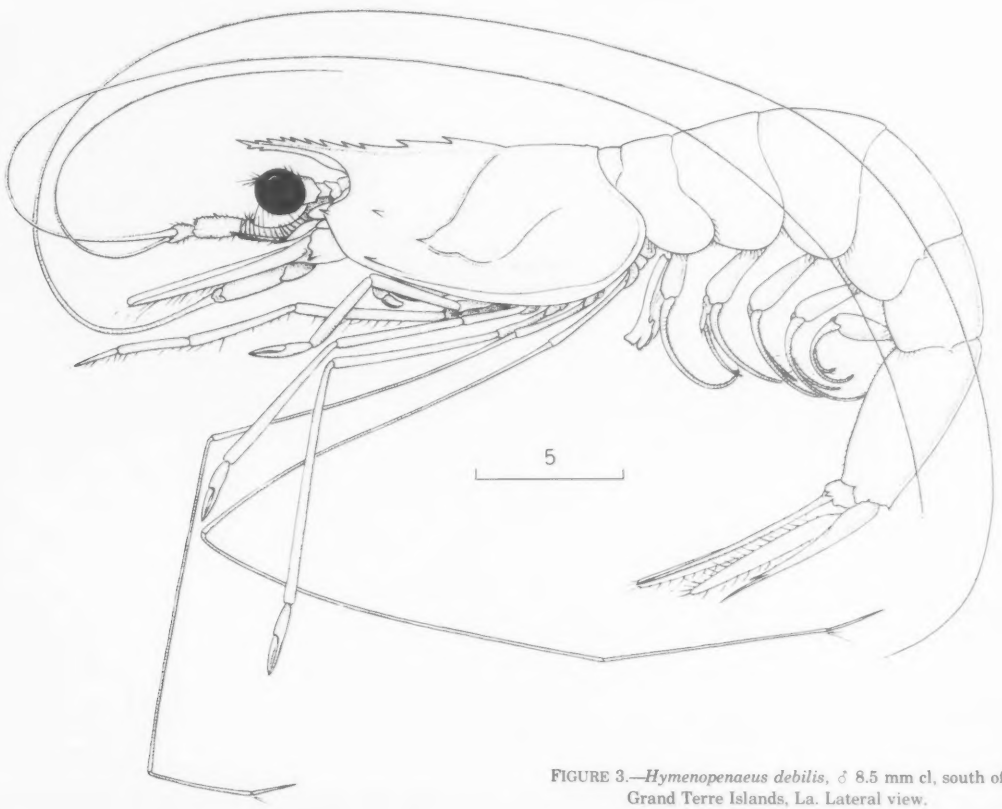

FIGURE 3.—*Hymenopenaeus debilis*, ♂ 8.5 mm cl, south of Grand Terre Islands, La. Lateral view.

PANAMA—1 ♀, RMNH, Golfo de los Mosquitos, 664-681 m, 21 July 1966, *Pillsbury* stn 447.

COLOMBIA—1 ♀, USNM, Golfo del Darién, 731 m, 28 May 1964, *Oregon* stn 4902.

VENEZUELA—1 ♀, USNM, E of San Juan de los Cayos, 421 m, 9 October 1963, *Oregon* stn 4439.

GUYANA—1 ♀, USNM, N of Fort York, 1,373-1,446 m, 15 July 1968, *Pillsbury* stn 689.

AZORES ISLANDS—1 ♀, MP, between Pico and São Jorge, 1,257 m, 15 August 1883, *Talisman* stn 139.

MOROCCO—4 ♂ 3 ♀ syntypes of *Haliporus debilis* var. *africanus* Bouvier, MP, off Mazaghan, 1,319 m, 14 June 1883, *Talisman* stn 21. 1 ♂ 9 ♀, MP, off Cap Cantin, 1,590 m, 17 June 1883, *Talisman* stn 33.

Description.–Body slender, integument thin, flexible and glabrous (Figure 3). Rostrum straight or slightly to strongly upturned, moderately long, reaching as far as distal end of second antennular article, its length not greater than 0.55 that of carapace, low and with dorsal and ventral margins straight. Rostral plus epigastric teeth $\frac{8\text{-}11}{0\text{-}4}$ (usually $\frac{9\text{-}10}{2}$, only 3% lacking ventral teeth); epigastric tooth located at about 0.4 cl from orbital margin, first rostral tooth (largest of all) at about 0.3 cl, and third above orbital margin; ventral teeth variously arranged, either closely grouped together or rather broadly spaced. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus, weak posteriorly, and followed by minute dorsal tubercle very near margin of carapace. Lateral spines on carapace slender and sharp: postorbital spine situated directly posterior to antennal and almost as long as branchiostegal; latter (largest of all) continuous with short, sharp basal carina; pterygostomian spine absent. Cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located at 0.55 cl from orbital margin, or slightly more posteriorly; hepatic sulcus with two ventral convexities, extending from below hepatic spine to anterior end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac carina strong, accompanying sulcus moderately deep; submarginal carina slender, extending along entire length of branchiostegite.

Eye (Figure 4B) with basal article produced mesially into small scale. Cornea broad, its greatest diameter approximately twice that of base of ocular peduncle (1.6-2.1, $\bar{x}$ 1.95; $N = 32$), and proportion of diameter to carapace length varying between 15.5 and 23.0, $\bar{x}$ 19.7. Cornea subreniform, with proximal margin oblique, slanting posterolaterally; an imaginary line drawn parallel to base of short ocular peduncle at level of its mesial tubercle intersects cornea.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, not quite reaching distomesial margin of cornea, falling short of distal margin of first antennular article, but its long distal setae overlapping base of second article; stylocerite rather short, its length about 0.6 of distance between its proximal extrem-

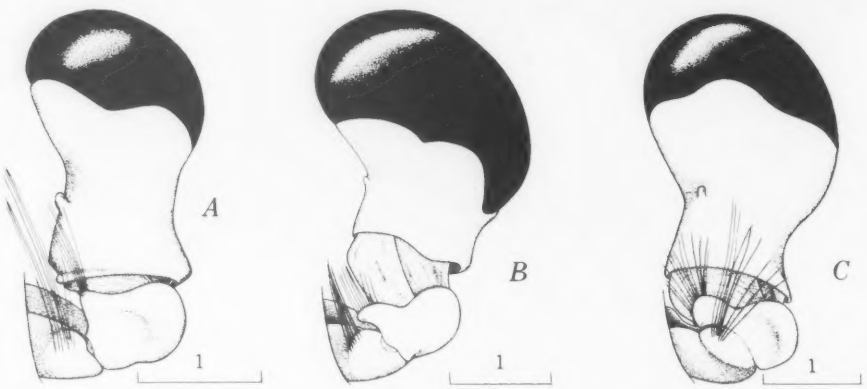

FIGURE 4.—Eyes. *A*, *Hymenopenaeus laevis*, ♀ 21 mm cl, off Martha's Vineyard, Mass. *B*, *Hymenopenaeus debilis*, ♂ 10.5 mm cl, northwest of Great Stirrup Cay, Bahama Islands. *C*, *Hymenopenaeus aphoticus*, ♀ 18 mm cl, northwest of Península de la Guajira, Colombia.

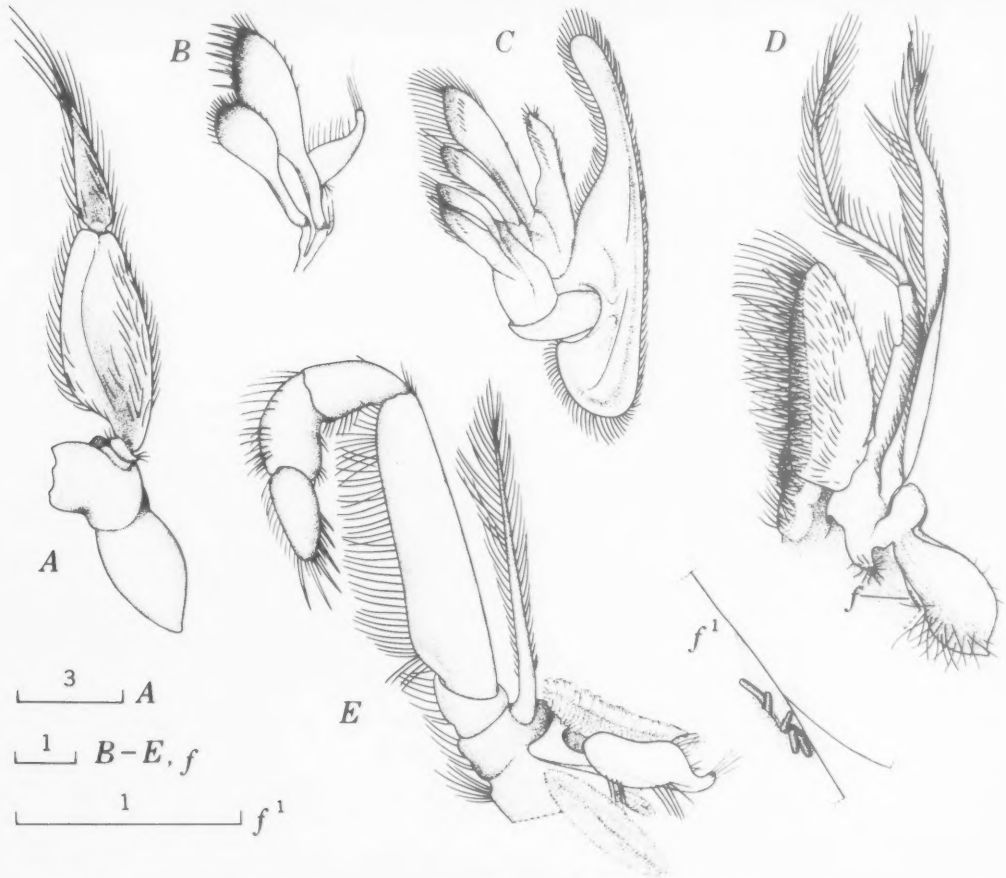

FIGURE 5.—*Hymenopenaeus debilis*, ♀ 19.5 mm cl, off Cape Kennedy, Fla. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *E*, Second maxilliped. *f*, Rudimentary arthrobranchia. f^1, Enlargement of *f* (all from left side).

ity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella very long and considerably unequal in length, ventral 2.15 and dorsal 7.5 times carapace length in shrimp 7 mm cl, and 1.7 and 5.5 times, respectively, in shrimp 10 mm cl. Scaphocerite overreaching antennular peduncle by as much as 0.25 of its own length; lateral rib ending in slender spine, falling short to slightly surpassing distal margin of lamella. Antennal flagellum incomplete in all specimens examined; however, in one individual about 35 mm tl, antennal length 155 mm, thus not less than 4.4 times total length of shrimp.

Mandibular palp (Figure 5*A*) reaching to about level of distal 0.2 of carpocerite; proximal article 2.4 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae, and first and second maxillipeds as illustrated (Figure 5*B-E*, virtually identical throughout genus); somite VII bearing rudimentary arthrobranchia at base of first maxilliped (Figure 5*Df-f*^{1}). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.7 that of propodus.

First pereopod, stoutest of five, reaching distal end of carpocerite or surpassing it by as much as length of dactyl. Second pereopod overreaching antennular peduncle by at least half length of dactyl or by entire propodus. Third pereopod exceeding antennular peduncle by length of dactyl,

propodus, and as much as 0.4 that of carpus. Fourth pereopod reaching beyond antennular peduncle by length of last three podomeres. Fifth pereopod exceeding antennular peduncle by length of last three podomeres or by latter and as much as 0.1 length of merus. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and either slender spine or no spine on ischium; second pereopod with small spine on basis. In female, coxa of third pereopod produced into large subtrapezoidal plate directed mesially, and bearing minute anteromesial spine in juveniles. In both sexes spine present on anteromesial corner of coxa of fifth pereopod, considerably stronger in males than in females, spine minute in latter and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina, and pair of minute spines posteroventrally. Telson with rather shallow median sulcus practically disappearing before reaching level of base of lateral spines; sulcus flanked by ridges, blunt anteriorly, sharp and slender posteriorly; terminal portion length 5-6 times basal width; lateral spines length 1.5-2.0 times basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson or slightly overreaching it; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with slender, distolateral spine, reaching as far as contiguous margin of ramus.

Petasma (Figures 2, 6*A*, *B*) with row of cincinnuli (hooklike structures along mesial margin of median lobes of petasma that serve to interlock its two halves) occupying only proximal 0.3 of median line, and entire terminal margin armed with spines; ventromedian lobule deeply cleft distally forming two elongate processes: mesial one subspatulate and armed with rather conspicuous spines mesially and minute ones distolaterally; lateral process subelliptical, raised inwardly in elongate prominence, and produced proximally in small auricular process lacking spinules; distal flap of ventrolateral lobule extending only to basal portion of lateral process, and turned strongly outward; ventral costa forming low prominence at base of, and imperceptibly merging with, flap.

Appendix masculina (Figure 6*C*, *D*) elevated in sharp mesial ridge and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae terminating in apical tuft of longer ones. Appendix interna elongate ovate, extending almost as far as appendix masculina, and also armed with apical tuft of setae. Ventrolateral spur of basal sclerite long, its length 0.7-0.8 that of appendix masculina.

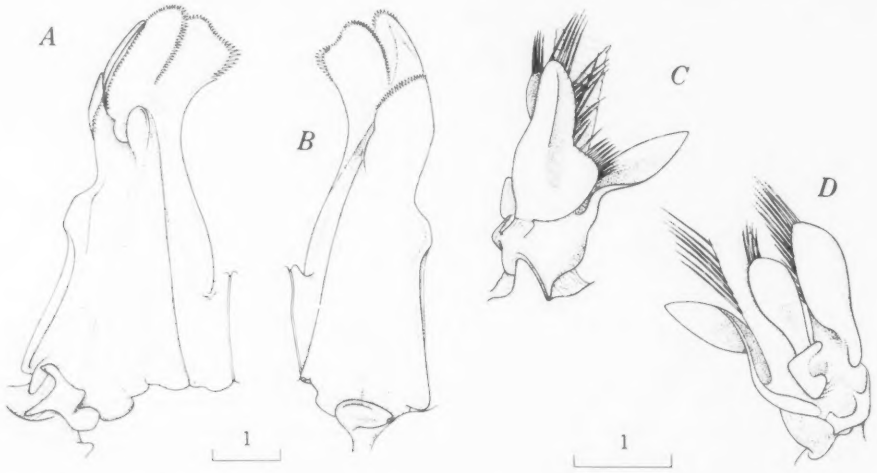

FIGURE 6.—*Hymenopenaeus debilis*, ♂ 13 mm cl, off Cape Kennedy, Fla. *A*, Petasma, dorsolateral view of left half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventral view.

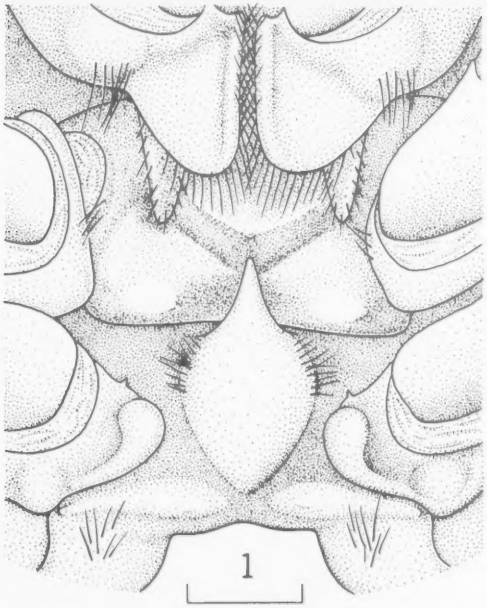

FIGURE 7.—*Hymenopenaeus debilis*, ♀ 15.5 mm cl, Dominica Island, Lesser Antilles. Thelycum, ventral view.

Thelycum (Figure 7) with median protuberance on sternite XIV pyriform, strongly produced anteriorly into acute, freely projecting apical portion overlapping, and closely appressed to, sternite XIII; latter bearing paired subtriangular elevations with bases raised in horizontal ridges flanking tip of protuberance on sternite XIV; anterior part of sternite XIII with setose transverse prominence; sternite XII bearing pair of large, setose, posterolateral horns reaching or slightly surpassing midlength of sternite XIII.

Photophores.–Six present on sternum: pair in elevated posterior margin of sternite XIII, just mesial to coxae of fourth pereopods; pair between second pleopods; single one between bases of fourth pereopods, and another between bases of fifth pleopods. Details of their structure given by Burkenroad (1936).

Color.–Bouvier (1908) on the basis of a water color illustration made at the moment of capture stated that the color is "d'un rouge-orange presque uniform." Burkenroad (1936) described fresh material as "transparent, speckled with minute scarlet chromatophores which were concentrated at the bases of the pleopods and uropods and at the tip of the telson. The ocular peduncle at the base of the cornea, the mouthparts, and the tip of the second maxillipede were scarlet. The stomach was red, the pleonic gut and nerve-cord orange; the gastric gland brownish, the ovary creamy (as seen through the overlying tissues). The eyes were reddish brown."

Maximum size.–Males, 55 mm tl; females, 78 mm tl (Bouvier 1908). Largest specimens examined by me: males 15.5 mm cl, 52 mm tl; females, 19.5 mm cl, 75 mm tl.

Geographic and bathymetric ranges.–Western Atlantic: from Hudson Canyon, New Jersey (39°55'N, 70°31'W) through the Gulf of Mexico and Caribbean Sea to Guyana (08°14'N, 57°38'W). Eastern Atlantic: Azores Islands and northwest Africa—from Cap Spartel, Morocco, to Cape Verde Islands, including Canary Islands (Figure 8). It has been found at depths (Figure 9) between 300 and 2,163 m (latter in Bouvier 1908).

Affinities.–Hymenopenaeus debilis closely resembles *H. aphoticus,* but differs from it in that the rostrum is usually armed with ventral teeth (only 3% of the specimens examined by me lack such teeth), and the sternum bears six photophores which are absent in *H. aphoticus.* The cornea is subreniform, and it is disposed such that its proximal margin is oblique to the basal margin of the ocular peduncle and an imaginary line extending from the medial tubercle parallel to the basal margin of the peduncle crosses its proximolateral extremity. The cornea (actually the entire eye) of *H. debilis* is also much larger than that of *H. aphoticus:* its maximum diameter about twice that of the basal margin of the peduncle, and the proportion of the diameter to the carapace length ranges from 15.5 to 22.0, averaging 19.7. Furthermore, in males of *H. debilis* the petasma exhibits larger distal processes than does that of *H. aphoticus,* but the lateral one is produced proximally in an auricle which is small and unarmed, and the proximomesial spinules on the free margin of the mesial process are only slightly longer than the remaining ones instead of considerably so as in *H. aphoticus.* Finally, the length of the ventrolateral spur borne by the sclerite at the base of the appendices masculina and interna is equivalent to 0.50-0.75 that of the appendix masculina. The thelyca of the two species are

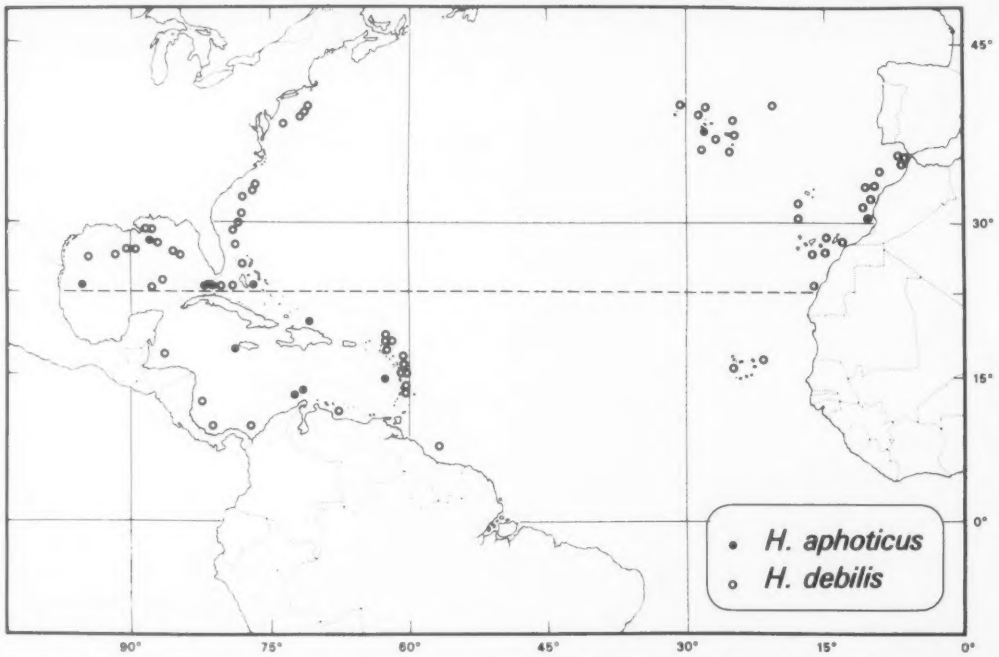

FIGURE 8.—Ranges of *Hymenopenaeus aphoticus* and *Hymenopenaeus debilis* based on published records and specimens personally examined.

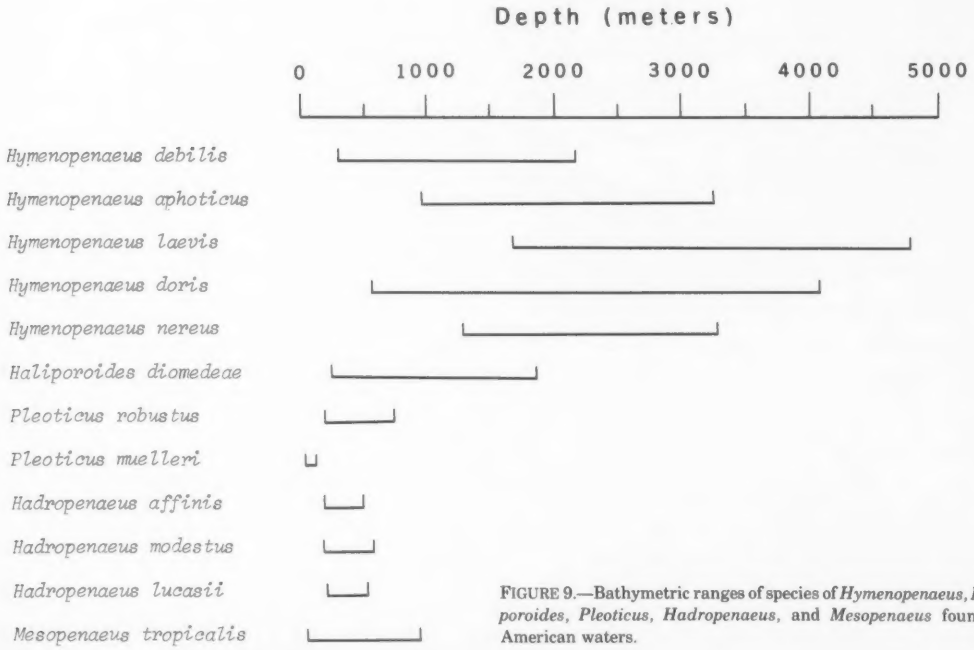

FIGURE 9.—Bathymetric ranges of species of *Hymenopenaeus*, *Haliporoides*, *Pleoticus*, *Hadropenaeus*, and *Mesopenaeus* found in American waters.

similar but the median protuberance of sternite XIV tends to be broader in *H. debilis* than in *H. aphoticus*.

According to Burkenroad (1936), in this species the proportion of the maximum diameter of the eye to carapace length is even greater than that given above, ranging between 19.3 and 26.9, $\bar{x}$ 22.3. My measurements of specimens studied by Burkenroad resulted in proportions not exceeding 23.0. This could be due to a slight reduction of the cornea caused by the preservatives, or the cornea is now deformed in the specimens with larger corneae examined by me.

Very similar to *H. debilis* is *H. chacei* which is known only from off West Africa. According to Crosnier and Forest (1969, 1973), these two species differ in that in *H. chacei* the ventral border of the rostrum is unarmed (actually, as stated above, 3% of the individuals of *H. debilis* examined by me lack such teeth), and no photophores are present. The cornea of *H. chacei* is narrower than that of *H. debilis*, in the former the ratio of the greatest diameter to the carapace length ranges from 13.2 to 16.0 ($\bar{x}$ 15.0), and it is disposed such that its proximolateral extremity lies slightly distal to the level of the medial tubercle.

A careful study of the western Atlantic specimens in which the rostrum is ventrally unarmed has left no doubt in my mind that they are *H. debilis*. *Hymenopenaeus chacei*, which typically lacks teeth on the ventral margin of the rostrum, is not represented in the extensive collections from the western Atlantic examined by me.

I have found that in males of *H. debilis* the disposition of both the mesial and lateral processes of the petasma varies from slightly to rather strongly inclined mesially, the former illustrated herein (Figure 6*A*, *B*), and the latter, illustrated by Crosnier and Forest (1973, plate 85, figure c-d, a male from Morocco). This variation is not associated with the size of the animal, and occurs throughout the entire range of the species in the western Atlantic. Males in which the processes are only slightly inclined mesially resemble those of *H. chacei* in which, according to Crosnier and Forest (1973), the roughly angular portion of the lateral process is typically directed forward. The males of the two species can still be distinguished by the size and armature of the auricular process of the petasma, which in *H. debilis* is very small and unarmed but relatively large in *H. chacei* and provided with marginal spinules (Crosnier and Forest 1969:546, figure 2).

Remarks.–The coordinates of the *Talisman* stations, cruise of 1883, where the material examined by me was collected, are given herein according to the data presented by Crosnier and Forest (1973).

The disposition of the third syntype, from southeast of Savannah Beach, Ga., caught at *Blake* stn 317 is unknown.

Hymenopenaeus aphoticus Burkenroad 1936

Figures 4C, 8-12

Hymenopenaeus aphoticus Burkenroad 1936:112, fig. 62, 65, 66, 67 [holotype: ♀, YPM 4556; type-locality: Turks Is Passage, 1,646-1,728 m, 21°15′40″N, 71°17′06″W, *Pawnee* stn 54]. Yokoya 1941:52. Crosnier and Forest 1969:547.

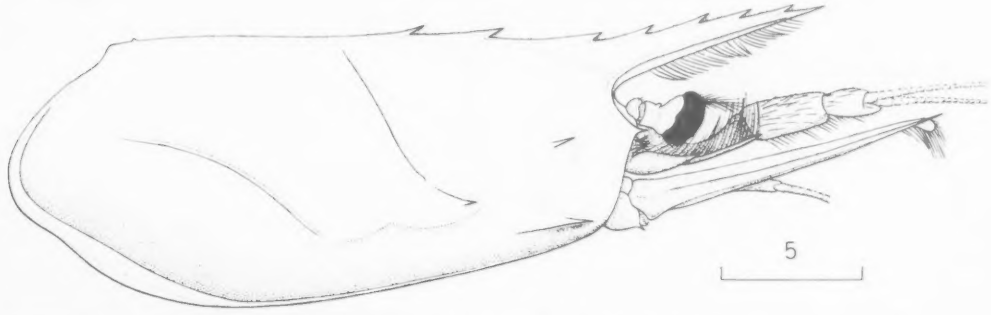

FIGURE 10.—*Hymenopenaeus aphoticus*, ♀ 18 mm cl, northwest of Península de la Guajira, Colombia. Cephalothorax, lateral view.

Roberts and Pequegnat 1970:31, fig. 3-1D. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:253, fig. 85e-f, 87c, 88b, 89c.

Material

UNITED STATES—Florida: 5 ♂ 3 ♀, RMNH-UMML, SW of Marquesas Keys, 1,373-1,428 m, 1 December 1964, *Gerda* stn 449. 2 ♂, USNM, SW of Marquesas Keys, 948-969 m, 29 August 1967, *Gerda* stn 858. 2 ♂, TAMU, NW of Dry Tortugas, 3,256 m, 29-30 July 1968, *Alaminos* stn 68A7-4E. 1 ♂, TAMU, SW of Cape San Blas, 1,097 m, 1 August 1968, *Alaminos* stn 68A7-7B. Alabama: 1 ♂, USNM, off Mobile Bay, 2,160 m, 3 March 1885, *Albatross* stn 2383. Texas: 1 ♀, TAMU, off Padre I, 1,399 m, 7 August 1969, *Alaminos* stn 69A11-7.

MEXICO—Tamaulipas: 1 ♀, USNM, off Boca de San Rafael, 1,668 m, 24 January 1970, *Oregon II* stn 10881. Veracruz: 1 ♂ 3 ♀, TAMU, NE of Tuxpan, 1,326 m, 24 August 1969, *Alaminos* stn 69A11-83. 1 ♂, TAMU, Bahía de Campeche, 2,122 m, 16 August 1969, *Alaminos* stn 69A11-44.

BAHAMA ISLANDS—1 ♂ paratype, YPM 4557, Tongue of the Ocean, "Wire 7000 feet" [2,134 m], 2 March 1927, *Pawnee* stn 11. ♂ holotype 1 ♀ paratype, YPM 4556, Turks I Passage, 1,646-1,728 m, 12 March 1927, *Pawnee* stn 54.

JAMAICA—1 ♀, USNM, W of South Negril Point, 1,591-1,829 m, 8 July 1970, *Pillsbury* stn 1238.

EASTERN CARIBBEAN—1 ♂ 6 ♀, USNM, S of I Aves, 1,249 m, 27 January 1884, *Albatross* stn 2117.

COLOMBIA—10 ♂ 6 ♀, USNM, NW of Península de la Guajira, 1,500 m, 27 July 1966, *Pillsbury* stn 454. 3 ♀, USNM, off Península de la Guajira, 2,500 m, 27 July 1966, *Pillsbury* stn 455.

Description.–Rostrum (Figure 10) slightly to rather strongly upturned, reaching as far as distal margin of second antennular article, its length about 0.45 that of carapace, and with both margins almost straight. Rostral plus epigastric teeth 7-8, sharp; epigastric tooth located at about 0.4 cl from orbital margin, first tooth (largest of all) at about 0.25, and second with apex at level of orbital margin; ventral teeth absent. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus, from there weak or indistinct porteriorly, and followed by minute tubercle located close to margin of carapace. Spines on lateral surface of carapace slender and sharp: postorbital spine situated directly posterior to antennal, and branchiostegal, largest of all, continuous with short, sharp carina; pterygostomian spine absent. Cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity placed at about 0.54 cl (or slightly farther anteriorly) from orbital margin; hepatic sulcus biconvex ventrally, running from base of hepatic spine to ventral end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac sulcus long, accompanying carina strong. Submarginal carina slender.

Eye (Figure 4*C*) with basal article produced mesially into small scale. Cornea comparatively narrow, its greatest diameter approximately 1.5 times that of base of ocular peduncle (1.25-1.75, $\bar{x}$ 1.55; N = 20), and proportion of diameter to carapace length varying between 10.0 and 12.5, $\bar{x}$ 11.1. Cornea hemispherical, with proximal margin subperpendicular to longitudinal axis of elongate ocular peduncle; an imaginary line drawn parallel to base of ocular peduncle at level of its mesial tubercle intersects lateral border far proximal to cornea.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling short of distal margin of first antennular article, but with long distal setae reaching base of second antennular article; stylocerite moderately long, extending 0.60-0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella long and unequal in length, ventral one 2.25 times as long as carapace in shrimp 17.5 mm cl; dorsal flagellum longer than ventral, unfortunately incomplete in all specimens examined. Scaphocerite length approximately 3.65 times maximum width, overreaching antennular peduncle by as much as 0.3 of its own length; lateral rib ending in slender spine extending to, or slightly surpassing, distal margin of lamella. Antennal flagellum long, at least 6.8 times total length of shrimp: male with total length of 45 mm bearing incomplete flagellum 300 mm long. Mandibular palp, maxillae and first two maxillipeds similar to those in *H. debilis* (see Figure 5). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus or by their lengths plus 0.1 that of carpus; length of dactyl about 0.7 that of propodus.

First pereopod, stoutest of five, reaching about distal end of carpocerite. Second pereopod overreaching antennular peduncle by, at least, tip of dactyl, or by as much as length of propodus. Third pereopod exceeding antennular peduncle by length of propodus and, at most, 0.4 that of carpus. Fourth pereopod overreaching antennular peduncle by length of distal three podomeres. Fifth pereopod exceeding antennular peduncle by length of distal three podomeres, or by length of

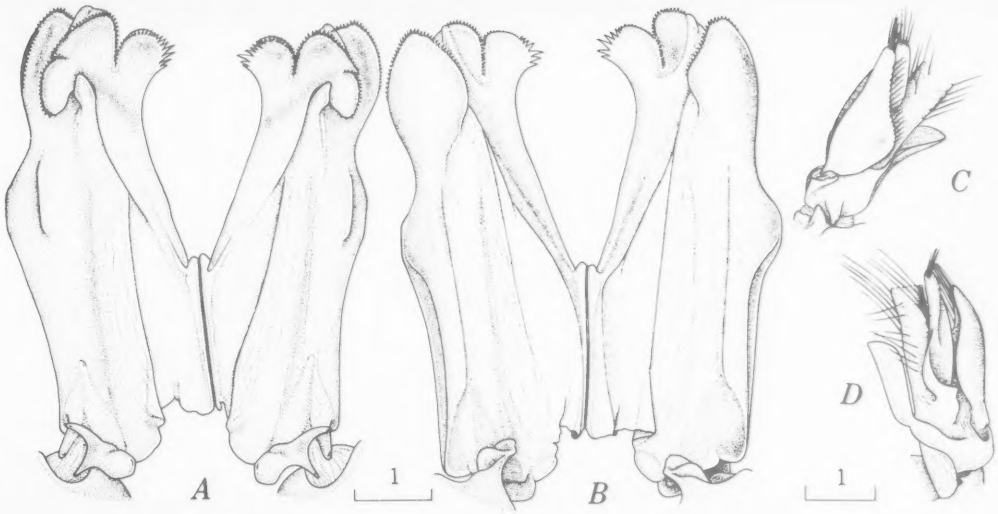

FIGURE 11.—*Hymenopenaeus aphoticus*, ♂ 14.5 mm cl, south of Isla Aves, eastern Caribbean. *A*, Petasma (extended), dorsolateral view. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

those podomeres and as much as 0.15 length of merus. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and long slender spine on ischium; second pereopod with small spine on basis. In female, coxa of third pereopod produced into subtrapezoidal plate, latter broadest mesially, disposed almost at right angle to podomere, and bearing minute anteromesial tooth in juvenile. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, considerably stronger in male than in female, in latter tooth minute and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina and pair of minute spines posteroventrally. Telson with rather shallow median sulcus extending posteriorly to level of base of lateral spines, and flanked by well-developed ridges; terminal portion length 5-6 times its basal width; lateral spines length 1.4-1.7 times basal width of terminal portion. Mesial ramus of uropod falling short of, or slightly overreaching, apex of telson; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with small, slender distolateral spine, falling slightly short of, or barely overreaching, contiguous margin of ramus.

Petasma (Figure 11*A*, *B*) with row of cincinnuli occupying proximal 0.4 of median line, and entire terminal margin armed with spines; ventromedian lobule distally cleft forming two moderately long processes: mesial one subtrapezoidal and armed with conspicuous spines mesially and minute ones distolaterally, lateral process subelliptical, raised inwardly in strong prominence, and produced proximally in rather large auricular process armed with marginal spinules; distal flap of ventrolateral lobule free, extending as far distally as lateral process, and only slightly turned outward; ventral costa forming low prominence at, and imperceptibly merging with, base of flap.

Appendix masculina (Figure 11*C*, *D*) strongly elevated along mesial portion and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae continuous with apical tuft of long setae. Appendix interna elongate-ovate, extending slightly farther distally than appendix masculina, and armed with apical tuft of setae. Ventrolateral spur short, its length not greater than 0.5 that of appendix masculina.

Thelycum (Figure 12) similar to that of *H. debilis* (see above).

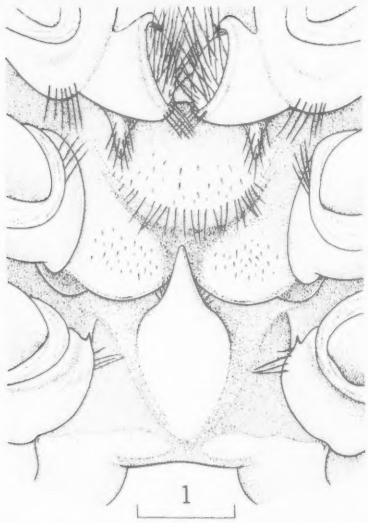

FIGURE 12.—*Hymenopenaeus aphoticus*, ♀ 18.5 mm cl, south of Isla Aves, eastern Caribbean. Thelycum, ventral view.

Maximum size.–Males: 18 mm cl; females: 19.5 mm cl.

Geographic and bathymetric ranges.–Western Atlantic: southwest Florida (23°56′N, 82°13′W), throughout the Gulf of Mexico, and the Caribbean Sea (12°55′N, 72°04′W). Eastern Atlantic (according to Crosnier and Forest 1973): south of the Azores Islands and off Morocco (Figure 8). It occurs at depths between about 950 m and 3,256 m (Figure 9).

Affinities.–Hymenopenaeus aphoticus is closely allied to *H. debilis*, but may be readily distinguished from it by the lack of teeth on the ventral margin of the rostrum, the absence of photophores, and the shape and disposition of the cornea (see above). In males of *H. aphoticus*, the petasma exhibits smaller distal processes than does that of *H. debilis*, and the auricle of the distolateral process is larger and armed with marginal spinules; also the proximomesial spinules on the free margin of the mesial process are considerably longer than the remaining ones, instead of only slightly longer as in *H.debilis*. Furthermore, in *H. aphoticus* the length of the ventrolateral spur at the base of the appendices masculina and interna is equivalent to only 0.5 that of the appendix masculina. Although the petasmata of the two species are different, the thelyca are markedly similar: the only detectable distinction is that the median protuberance on sternite XIV tends to be narrower in *H. aphoticus* than in *H. debilis*.

Remarks.–In examining a lot of seven specimens of *H. aphoticus* obtained at *Albatross* stn 2117, Roberts and Pequegnat (1970) misread the number on the accompanying label. They stated that in the Smithsonian Institution there is a lot of *H. aphoticus* taken by the *Albatross* at "Stn 2217, 1889" in the western Atlantic. Actually, the number on the label is 2117 for which the coordinates are 15°24′40″N, 63°31′30″W (south of Isla Aves in the eastern Caribbean, visited by the *Albatross* in 1884) instead of 2217, an 1889 station situated at 39°47′20″N, 69°34′15″W, which is off New Jersey. Because the authors thought the lot had been obtained at the latter locality, they stated that the species ranges as far north as 39°47′ (actually it has not been recorded from off the Atlantic coast of the United States). The misreading of the label also caused them to be unaware of the Caribbean record for *H. aphoticus* and to state that "It may eventually be found in the Caribbean also."

Hymenopenaeus laevis (Bate 1881)

Figures 4A, 9, 13-16

Haliporus laevis Bate 1881:185 [syntypes: 2 ♀, BMNH; type-locality: SW of Sierra Leone (W of Cameroon), 2°25′N, 20°01′W, 2,500 fm (4,573 m), *Challenger* stn 104]. Bate 1888:289, pl. 42, fig. 2. Bouvier 1906b:3; 1908:80. de Man 1911:7. Estampador 1937:494.

Hymenopenaeus microps Smith 1884:413, pl. 10, fig. 1 [syntypes: 1 ♀, USNM 7148, E of Georges Bank, Mass., 41°13′00″N, 60°00′50″W, 906 fm (1,657 m), *Albatross* stn 2076; 1 ♀ oral appendages, YPM 4559, off New Jersey, 38°50′00″N, 69°23′30″W, 1,731 fm (3,166 m), *Albatross* stn 2037]. Smith 1886:189; 1887:688, pl. 16, fig. 8. Wood-Mason 1891:277. Wood-Mason and Alcock 1891:188.

Haliporus microps. Alcock and Anderson 1894: 146. Alcock 1901:25. Bouvier 1906a:255; 1906b: 3; 1908:80. de Man 1911:7. Fowler 1912:543.

Hymenopeneus microps. Alcock 1899a:30.

Haliporus androgynus Bouvier 1906a:253 [syntypes: 1 ♀, MP, between "Dakar et la Praya," (off Mauritania), 16°38′N, 20°44′W, 3,200 m, *Talisman* stn 105. 1 ♀, MP, between "Dakar et

la Praya," (off Senegal), 15°48′N, 20°23′W, 3,655 m, *Talisman* stn 106]. Bouvier 1906b:3; 1908:80. de Man 1911:7.

Haliporus sp. Lenz and Strunck 1914:300, fig. 2.

Hymenopenaeus laevis. Burkenroad 1936:106; 1938:61. Anderson and Lindner 1945:289.Crosnier and Forest 1973:253, fig. 82a, 83b.

Material

UNITED STATES—Massachusetts: 1 ♀ syntype of *H. microps* Smith, USNM 7148, E of Georges Bank, 1,657 m, 4 September 1883, *Albatross* stn 2076. 1 ♀, USNM, SE of Martha's Vineyard, 2,844 m, 30 July 1883, *Albatross* stn 2042. New Jersey: 1 ♀, USNM, off Atlantic City (Hudson Canyon), 1,977 m, 9 August 1885, *Albatross* stn 2550. 1 ♀ [oral appendages] syntype of *H. microps* Smith, YPM 4559, 3,166 m, 18 July 1883, *Albatross* stn 2037. Virginia: 4 ♀, USNM, 1 ♀, AMNH, E of Delmarva Peninsula, 4,792 m, 29 August 1885, *Albatross* stn 2566. North Carolina: 1 ♀ 1 ♀, USNM, NE of Kitty Hawk, 4,708 m, 8 September 1884, *Albatross* stn 2224.

BERMUDA ISLANDS—1 ♂, YPM, N of Bermuda Is, "10000 feet wire" [3,048 m], 20 April 1927, *Pawnee* stn 58. 1 ♀, YPM, N of Bermuda Is, "8000 feet wire" [2,438 m], 21 April 1927, *Pawnee* stn 59.

BAHAMA ISLANDS—1 ♂ 2 ♀, YPM, Turks I Passage, "8000 feet wire" [2,438 m], 11 April 1927, *Pawnee* stn 52. 2 ♀, YPM, Turks I Passage, "6500 feet wire" [1,981 m], 13 April 1927, *Pawnee* stn 56.

MAURITANIA—1 ♀ syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Mauritania], 3,200 m, 18 July 1883, *Talisman* stn 105.

SENEGAL—1 ♀ syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Senegal], 3,655 m, 19 July 1883, *Talisman* stn 106.

CAMEROON—2 ♀ syntypes, BMNH, "south-west of Sierra Leone," 2°25′N, 20°1′W [W of Cameroon], 4,573 m, 23 August 1873, *Challenger* stn 104.

PHILIPPINE ISLANDS—1 ♀, BMNH, off Manila, 1,920 m, 13 November 1874, *Challenger* stn 205.

Description.–Rostrum (Figure 13) short, its length about 0.2 that of carapace, falling short of distal margin of first antennular article, horizontal or slightly upturned, tapering to very sharp tip, and with ventral margin slightly sinuous. Rostral plus epigastric teeth 7-9, sharp; epigastric tooth situated at about 0.4 cl from orbital margin, first rostral tooth (largest of all) at approximately 0.3, and third opposite to, or slightly forward of, orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina well defined to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine small; postorbital (situated directly posterior to relatively small antennal spine), branchiostegal, and pterygostomian spines continuous with sharp basal carina. Cervical carina sharp, notched dorsal to hepatic spine; cervical sulcus deep, extending to, but not crossing postrostral carina, its dorsal extremity located at or slightly posterior to midlength of carapace; hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, virtually reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye (Figure 4*A*) with basal article produced mesially into barely distinct scale; ocular peduncle long; cornea comparatively narrow, its greatest diameter about 1.4 times that of base of ocular peduncle, its proximal margin only slightly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling considerably short of distal margin of first antennular article; stylocerite short, extending only 0.4-0.5 of distance between its prox-

FIGURE 13.—*Hymenopenaeus laevis*, ♀12.5 mm cl, Turks Island Passage, Bahama Islands. Cephalothorax, lateral view.

imal extremity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella incomplete in all specimens examined by me, according to Bate (1888) "about two-thirds the length of the animal." Scaphocerite reaching as far as antennular peduncle or barely overreaching it; lateral rib ending in slender spine falling slightly short of, or slightly overreaching, distal margin. Antennal flagellum broken in specimens examined by me, according to Bate (1888) "rather longer than the animal." Mandibular palp reaching to about distal 0.25 of carpocerite. Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.75 that of propodus.

First pereopod extending to about distal end of carpocerite. Second pereopod reaching distal end of antennular peduncle, or exceeding it by as much as length of dactyl. Third pereopod surpassing antennular peduncle by length of dactyl, propodus, and at least 0.25 that of carpus. Fourth pereopod exceeding antennular peduncle by length of dactyl, propodus, and 0.4-0.5 that of carpus. Fifth pereopod overreaching antennular peduncle by length of dactyl, propodus, and 0.75-0.80 that of carpus. Pereopods increasing in length from first to fifth. First pereopod with minute spine on basis, and small one on ischium; second pereopod with small spine on basis. Coxal plate of third pereopod in females broadening mesially and produced posteriorly into setose, rounded lobe. Tooth present on anteromesial corner of coxa of fifth pereopod in both sexes, strong and blunt in males, minute, and borne by rounded coxal plate in females.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision, sometimes bearing minute spine at base; sixth somite about twice as long as high, armed with small, sharp spine at posterior end of carina and pair of posteroventral spines. Telson with median sulcus deep anteriorly, increasingly shallower posteriorly to level of base of lateral spines, flanked by paired ridges, blunt anteriorly, sharp posteriorly; length of terminal portion about 5 times its basal width; spines moderately long, 1.20-1.35 basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson, or overreaching it by no more than 0.1 of its length; lateral ramus exceeding mesial ramus by as much as 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma (Figure 14*A*, *B*) with row of cincinnuli occupying about proximal 0.5 of median line, its entire terminal margin lacking spines; ventromedian lobule bearing two, rarely three, small, triangular processes distomesially, and short,

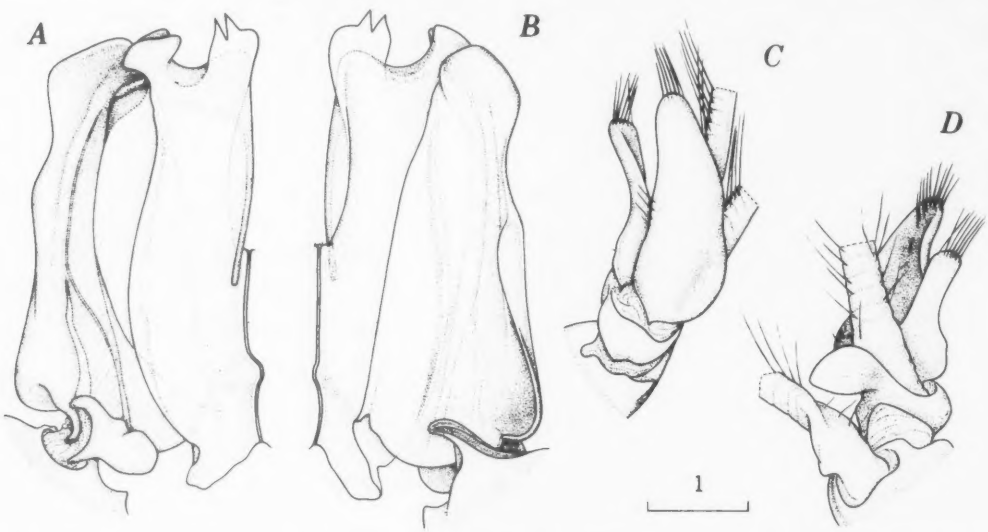

FIGURE 14.—*Hymenopenaeus laevis*, ♂ 15 mm cl, Turks Island Passage, Bahama Islands. *A*, Petasma, dorsolateral view of left half. *B*, Ventrolateral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

rigid, transversely elliptical process distolaterally; distal part of ventrolateral lobule roughly elliptical and strongly trending toward ventromedian lobule; ventral costa broad proximally, considerably narrower distally and, in young, ending in minute marginal spine projecting from base of elliptical part of ventrolateral lobule.

Appendix masculina (Figure 14*C, D*) with proximal part produced laterally into rounded lobe bearing row of long setae on distal margin continuous with row extending along midventral line of narrow distal portion; latter armed with apical tuft of long setae; appendix interna abruptly narrowing from rounded base and bearing apical tuft of long setae; ventrolateral spur with distal part subovate, bearing longitudinal submarginal rib on dorsal surface.

Thelycum (Figure 15) with median protuberance on sternite XIV setose, pyramidal, and with triangular base, its apical portion produced into short ventrally directed projection; median lamella projecting vertically from posterior margin of sternite XIII, flat, its distal margin slightly to deeply emarginate (emargination angular or curved), lateral margins straight or slightly concave; posterior part of sternite XII bearing paired, setose horns overreaching midlength of sternite XIII.

Maximum size.–Males: 15 mm cl; females: 22 mm cl.

Geographic and bathymetric ranges.–Western Atlantic: from off Georges Bank, Mass. (41°13′00″N, 60°00′50″W), to the Bahamas (21°20′15″N, 71°13′20″W), including the Bermudas (Figure 16). Eastern Atlantic: from west of Mauritania to off Equatorial Guinea (Bate 1888). Indo-West Pacific: in the Arabian Sea (Laccadive Sea, Wood-Mason and Alcock 1891), the Bay of Bengal (off Andaman Islands,Wood-Mason 1891; Alcock 1901), and the Philippines (Bate 1888). If the record of "*Haliporus* sp." by Lenz and Strunck (1914) is actually one for this species, its range off west Africa reaches farther south, at least to off Liberia (0°39′N, 18°57′W). This shrimp has been found at depths between 1,657 and 4,792 m (Figure 9). Its habitat together with its small size are most probably responsible for the few collections available.

Affinities.–*Hymenopenaeus laevis* is closely allied to the American Pacific *H. doris* and *H. nereus*, and to the Indo-West Pacific *H. sewelli*. These four species form the compact section 2 of Burkenroad's group IV. They are the only members of the genus which possess both branchiostegal and pterygostomian spines.

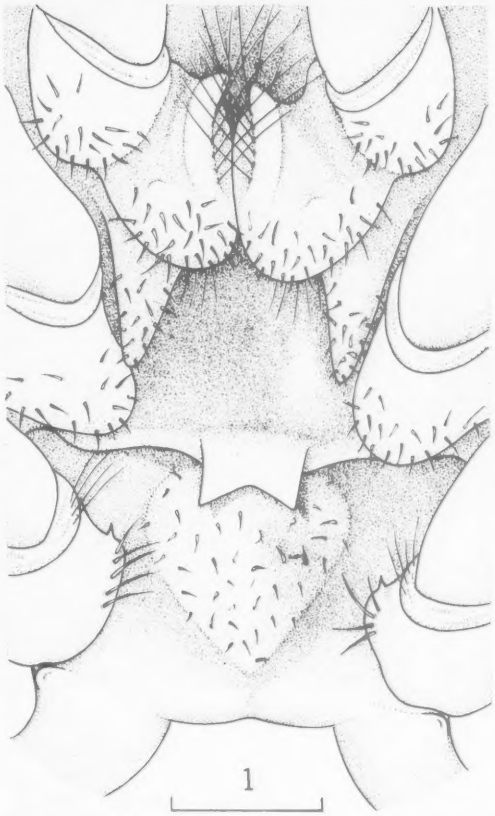

FIGURE 15.—*Hymenopenaeus laevis*, ♀ 17 mm cl, Turks Island Passage, Bahama Islands. Thelycum, ventral view.

Females of *H. laevis* differ strikingly from those of *H. nereus* in the structure of the thelycum. In those of *H. nereus*, the median lamella of sternite XIII is directed anteriorly, and has arched or sinuous lateral margins converging basally. Furthermore, in *H. nereus* the median lamella is flanked by paired, caudally inclined processes, which are lacking in *H. laevis*, and sternite XIV is raised in a median longitudinal ridge, very different from the strong pyramidal prominence present in the latter. This shrimp, in turn, can be separated readily from *H. doris* by the median lamella of

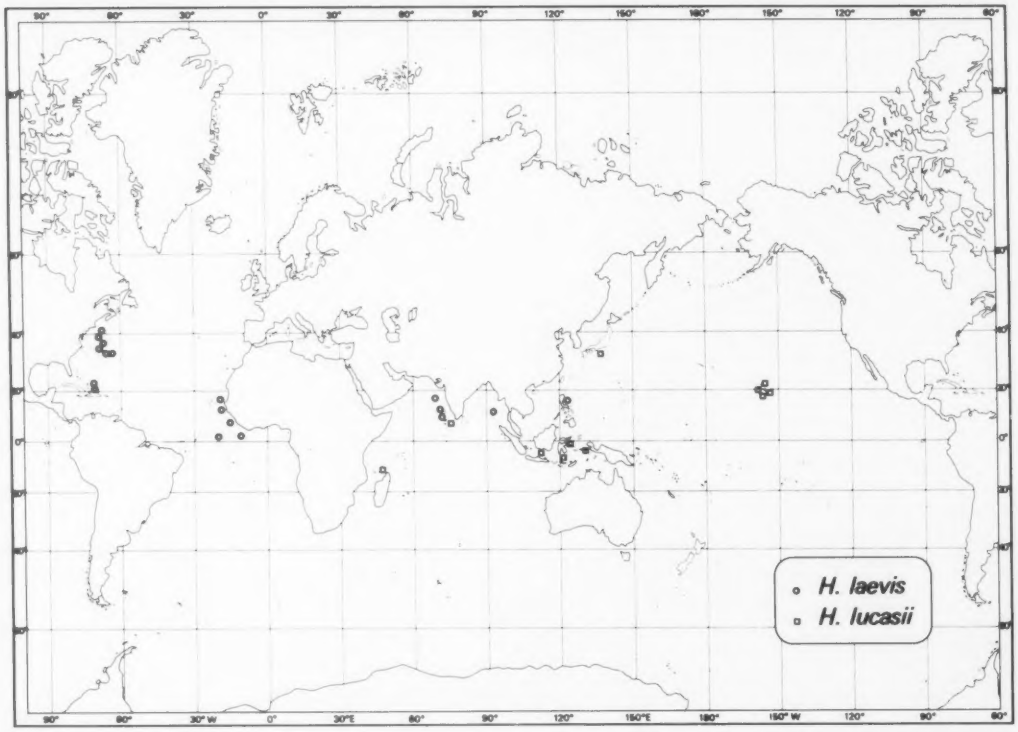

FIGURE 16.—Ranges of *Hymenopenaeus laevis* and *Hadropenaeus lucasii* based on published records and specimens personally examined.

sternite XIII which in the latter is concave anteriorly, has a usually convex, never emarginate, distal margin. The median lamella also is flanked by paired ridges which are triangular in cross section and as high as the lamella. Furthermore, in *H. doris*, sternite XIV bears a median protuberance which is strongly produced in an elongate projection lying quite close to the lamella.

Males of *H. laevis* differ markedly from those of *H. nereus* in that the petasma of the latter bears a single, large, mesial process distally which, moreover, is subrectangular, directed perpendicular to the main axis of the petasma, and armed with long spines; in addition, the lateral process is directed distomesially instead of extending transversely, and is strongly curved outward. Finally, the distal part of the ventrolateral lobule of the petasma is acuminate instead of subelliptical, and is only slightly inclined toward the ventromedian lobule.

As previously indicated by Burkenroad (1936) and Crosnier and Forest (1973), females of this species exhibit considerable variation in the shape and size of the median lamella on sternite XIII. Extending ventrally, it may be short or long, reaching between midheight and slightly beyond the apex of the median protuberance on sternite XIV. In the young, the lamella is truncate, and in the adult it ranges from shallow to deeply emarginate distally, forming a fork with the projections varying from rather broadly triangular to spinelike.

In the young male, as stated above, the petasma bears a minute subdistal spine at the free margin of the costa, and the more mesial of the two distal projections of the ventromedian lobule is at best only slightly developed.

Remarks.–Burkenroad (1936) presented a detailed account of the external morphology and an enlightened analysis of the taxonomic status of this species; as a result, he placed two well-known scientific names, *H. microps* and *H. androgynus*,

in the synonymy of *H. laevis*. In this same contribution, Burkenroad mentioned a "minute denticle of variable size" posterior to the epigastric tooth, and suggested that it is "probably the remains of the larval anterior dorsal organ." In that location, however, I have observed nothing more than an extremely slight elevation of the postrostral carina, and that only in two specimens. Had this feature not been mentioned by Burkenroad, I should have overlooked it, and, after observing it, I believe it to be insignificant.

Bouvier (1906b) described *Haliporus androgynus* on the basis of two specimens which bear, in addition to a fully developed thelycum, both petasma and appendices masculinae. Burkenroad (1936) stated that the simultaneous presence of the female and male external genitalia in these specimens probably represents an abnormality. Recently, Crosnier and Forest (1973) indicated that this combination of secondary sexual characters could represent an expression of protandric hermaphroditism, as reported by Heegaard (1967) in *Solenocera membranacea* (Risso 1816). They added that in a rather large number of penaeids the maximum size of males corresponds to the minimum size of females. It should be noted, however, that Burkenroad (1936) cited a female of *H. laevis*, also examined by me, with a carapace length of 8 mm, which is about half the length of the largest known male, 15 mm cl.

In the two syntypes of *H. androgynus*, which have a carapace length of about 20 mm, the petasmata are shorter than in other males of equal size, and exhibit and armature with these juvenile features. In one of the specimens, the mesial projection is extremely small, whereas the lateral projection and the distolateral process are well developed; in the other, the mesial projection is distinct, the lateral one very small, the distolateral process is well developed, and a subdistal spine is present on the free margin of the ventral costa.

Hymenopenaeus doris (Faxon 1893)

Figures 9, 17, 18A, 19-20

Haliporus doris Faxon 1893:214 [syntypes: 4 ♀, MCZ 4648, off Cabo Velas Costa Rica, 10°14′N, 96°28′W, 2,232 fm (4,082 m), 8 April 1891, *Albatross* stn 3414. 1 ♀, USNM 21182, S of Punta Maldonado, Guerrero, Mexico, 14°46′N, 98°40′W, 1,879 fm (3,437 m), 10 April 1891, *Albatross* stn 3415]. Faxon 1895:191, pl. 49, fig. 1-1c. Bouvier 1906b:3; 1908:80. de Man 1911:7

Hymenopenaeus doris. Burkenroad 1936:104; 1938:60. Crosnier and Forest 1973:256, fig. 83d.

Aliporus doris. del Solar C. 1972:4.

Material

MEXICO—Territorio de Baja California: 1 ♀, USNM, off Punta Chivato, Golfo de California, 1,567 m, 20 March 1889, *Albatross* stn 3009. 1 ♀, AMNH, 54 km off Punta Arena, mouth of Golfo de California, 914 m, 29 April 1936, Templeton Crocker Expedition stn 159 T-3 [station data from Beebe 1937].

COSTA RICA—4 ♀ syntypes, MCZ 4648, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414. 1 ♀, USNM, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414.

Description.–Rostrum (Figure 17) relatively short, its length about 0.2 that of carapace, reaching between base and midlength of second antennular article, upturned, tapering to sharp tip, and with ventral margin straight. Rostral plus epigastric teeth 7-8, sharp; epigastric tooth situated about 0.4 cl from orbital margin, first rostral tooth (largest of all) at approximately 0.3, and base of

FIGURE 17.—*Hymenopenaeus doris*, syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. Cephalothorax, lateral view.

third in line with orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine slender and sharp like other lateral spines on carapace; postorbital (situated directly posterior to antennal), pterygostomian, and branchiostegal spines with sharp basal carina, that continuous with branchiostegal spine merging with hepatic carina. Cervical carina strong, extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace; hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running from posterior extremity of hepatic sulcus to posterior margin of carapace; branchiocardiac carina also long, reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye as illustrated (Figure 18*A*).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema extending to distal margin of eye, but falling short of distal end of first antennular article; stylocerite short, extending 0.5 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella incomplete in specimens examined.

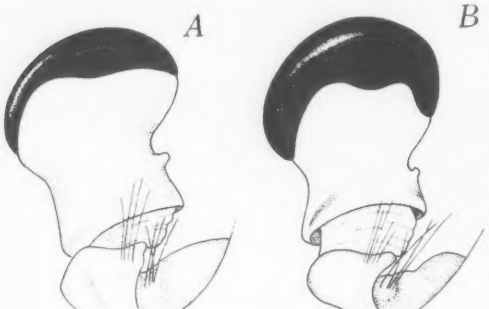

FIGURE 18.—Eyes. *A, Hymenopenaeus doris,* syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. *B, Hymenopenaeus nereus,* syntype ♀ 21.5 mm cl, south of Cabo Blanco, Costa Rica.

Scaphocerite overreaching antennular peduncle by 0.25 of its own length; lateral rib ending in slender spine, extending to distal margin of lamella. Antennal flagellum broken in specimens studied. Mandibular palp reaching distal 0.2 of carpocerite; proximal article about 2.5 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First maxilliped with single rudimentary arthrobranchia at base. Third maxilliped reaching beyond antennular peduncle by dactyl and almost entire length of propodus; length of dactyl about 0.65 that of propodus.

First pereopod extending to distal end of carpocerite. Second pereopod overreaching antennular peduncle by length of propodus. Third pereopod exceeding antennular peduncle by length of propodus and about 0.33 that of carpus. Fourth pereopod overreaching antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth pereopod reaching beyond antennular peduncle by length of distal three podomeres. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and slender spine on ischium; second pereopod with minute spine on basis. In female, coxa of third pereopod produced into large, subtrapezoidal plate, broadest mesially, and disposed almost at right angle to podomere; coxa of fifth pereopod armed with minute anteromesial tooth.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter two somites with short median incision; sixth somite very elongate, 2.5 times as long as high, bearing small, sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus deep anteriorly, quite shallow posteriorly, and flanked by low, sharp ridges; terminal portion length 5-6 times basal width; lateral spines short, their length about 1.5 times basal width of terminal portion. In only specimen with complete uropod, mesial ramus falling short of apex of telson; lateral ramus overreaching mesial ramus by 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma unknown; males not recorded.

Thelycum (Figure 19*A, B*) with median protuberance on sternite XIV subpyramidal, with subtriangular base and apical portion strongly produced into elongate, acute projection directed ventrally or anteroventrally, and lying quite near

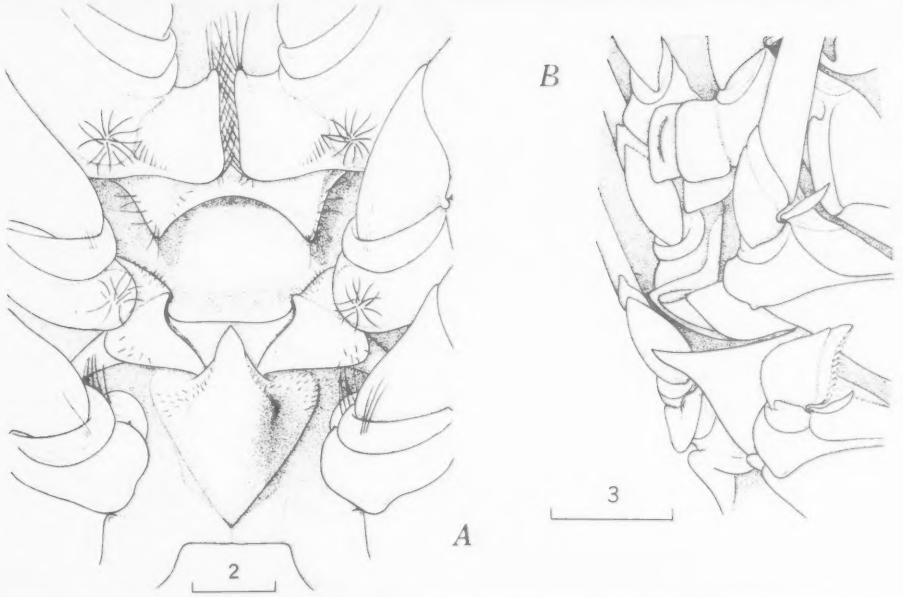

FIGURE 19.—*Hymenopenaeus doris*, syntype ♀ 32.5 mm cl, off Cabo Velas, Costa Rica. *A*, Thelycum,ventral view. *B*, syntype ♀ 32 mm cl, same locality, thelycum, ventrolateral view (setae omitted).

median lamella of sternite XIII; lamella, projecting vertically, heavily sclerotized, excavate anteriorly, with distal margin truncate or convex; pair of high ridges (triangular in cross section) flanking and posteriorly overlapping median lamella; posterior part of sternite XII bearing paired short, blunt horns covered by long setae.

Maximum size.–Females: 33.5 mm cl.

Geographic and bathymetric ranges.–Eastern Pacific: from off Punta Chivato (27°09′N, 111°42′W), Gulf of California, to Isla del Coco, Costa Rica (Figure 20), at depths between 549 and 4,082 m (Figure 9). Burkenroad (1938) cited the depth, 300 fm (549 m), at which one juvenile specimen was taken from the *Arcturus* off Isla del Coco, but did not give the coordinates of the locality. Beebe (1926), however, indicated that the various hauls from the *Arcturus* in the area were made slightly south of Isla del Coco, and cited the following coordinates: 4°30′N, 87°00′W.

Affinities.–Hymenopenaeus doris is closely allied to *H. nereus*, the only other member of the genus known from the American Pacific. Females of the two species can be distinguished readily by thelycal features: in *H. doris* a strong median protuberance is present on sternite XIV, and the lamella on the posterior margin of sternite XIII is disposed vertically, is deeply excavate anteriorly, and its distal margin is truncate or convex; in *H. nereus* only a median longitudinal rib is present on sternite XIV, and the lamella on XIII is inclined anteriorly, is flattened, and its distal margin is concave. Finally, in *H. doris* the lamella is flanked by high ridges whereas in *H. nereus* these are replaced by flattened, scalelike processes directed caudally.

Remarks.–Only nine specimens of *H. doris* are known. Seven, five of which are syntypes, were collected by the *Albatross* (1891); one of these (not designated by Faxon as part of the type-series) was taken with four syntypes at *Albatross* stn 3414, and the seventh was caught in the Gulf of California at *Albatross* stn 3009. Two additional specimens were cited by Burkenroad (1938), a juvenile female from the mouth of the Gulf of California, and another juvenile from off Isla del Coco (Costa Rica) taken by the *Arcturus* in 300 fm (549 m).

FIGURE 20.—Ranges of *Hymenopenaeus doris*, *Hymenopenaeus nereus*, and *Haliporoides diomedeae* based on published records and specimens personally examined.

Hymenopenaeus nereus (Faxon 1893)

Figures 9, 18B, 20-23

Haliporus nereus Faxon 1893:213 [syntypes: 1 ♀, MCZ 4645, S of Cabo Blanco, Costa Rica, 5°30′N, 86°45′W, 1,067 fm (1,952 m), 27 February 1891, *Albatross* stn 3366. 1 ♀, USNM 21177, S of Morro de Puercos, Panama, 7°06′15″N, 80°34′00″W, 695 fm (1,271 m), 23 February 1891, *Albatross* stn 3353. 2 ♀, USNM 21178, off Pen de Azuero, Panama, 6°21′N, 80°41′W, 1,793 fm (3,279 m), 7 March 1891, *Albatross* stn 3382. 1 ♂ 2 ♀, USNM 21180, NW of Is Galápagos, Ecuador, 2°34′N, 92°06′W, 1,360 fm (2,487 m), 5 April 1891, *Albatross* stn 3413. 2 ♀, MCZ 4646, NW of Punta Galera, Ecuador, 1°07′N, 80°21′W, 1,573 fm (2,877 m), 23 March 1891, *Albatross* stn 3398. 1 ♂, MCZ 4647, NW of Punta Galera, Ecuador, 1°07′N, 81°04′W, 1,740 fm (3,182 m), 24 March 1891, *Albatross* stn 3399. 2 ♀, USNM 21179, E of Is Galápagos, Ecuador, 00°36′S, 86°46′W, 1,322 fm (2,418 m), 27 March 1891, *Albatross* stn 3400. 1 ♀, Is Galápagos, Ecuador, 00°04′00″S, 90°24′30″W, 885 fm (1,619 m), 3 April 1891, *Albatross* stn 3407]. Faxon 1895: 189, pl. 48, fig. 1-1d. Bouvier 1906b:3; 1908:80. de Man 1911:7.

Hymenopenaeus nereus. Burkenroad 1936:104; 1938:60. Ramadan 1938:60. Crosnier and Forest 1973:256, fig. 83c.

Material.–Syntypes, which are the only material ever recorded; 1 ♀ collected at *Albatross* stn 3407 has not been located.

Description.–Rostrum (Figure 21) relatively short, its length about 0.3 that of carapace, reaching about midlength of second antennular article, horizontal or slightly upturned, tapering to sharp tip, and with dorsal and ventral margins straight. Rostral plus epigastric teeth 8; epigastric tooth situated at about 0.4 cl from orbital margin, first rostral (largest of all) at approximately 0.3, and base of third opposite to orbital margin. Adrostral carina low, sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine slender and sharp, like other lateral spines on carapace; postorbital (located directly posterior to antennal), pterygostomian, and branchiostegal continuous with sharp basal carina, that continuous with branchiostegal merging with sharp hepatic carina. Cervical carina strong; sulcus extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace; hepatic carina sharp, its accompanying sulcus deep; additional short carina lying dorsal and parallel to hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, extending nearly to posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac; submarginal carina well defined, running along entire length of branchiostegite.

Eye as illustrated (Figure 18*B*).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema broad, reaching distal margin of eye, but falling short of distal margin of first antennular article; stylocerite short, extending 0.45-0.50 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long and sharp; second antennular article with transverse row of sharp spines near distal margin; antennular fla-

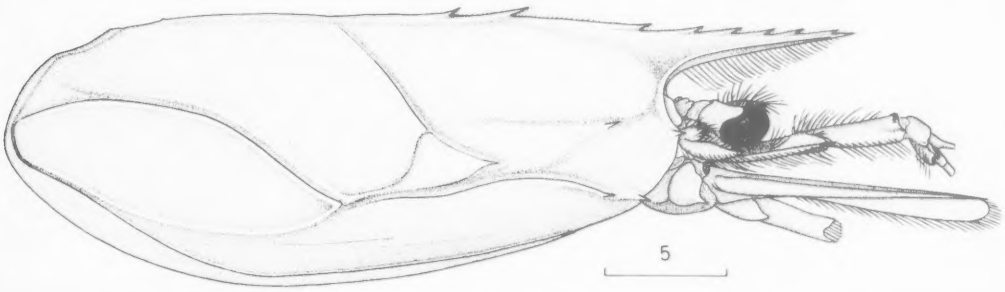

FIGURE 21.—*Hymenopenaeus nereus*, syntype ♀ 23.5 mm cl, northwest of Islas Galápagos. Cephalothorax, lateral view.

gella incomplete in specimens examined; however, in Faxon's (1895) illustration both subequal, about 1.25 times as long as carapace. Scaphocerite overreaching antennular peduncle by as much as 0.3 of its own length, with lateral rib ending in sharp, slender spine reaching, or overreaching, distal margin of lamella. Mandibular palp extending to distal 0.3 of carpocerite; proximal article about 2.6 times as long as wide. Third maxilliped reaching beyond antennular peduncle by length of dactyl and about 0.5 that of propodus; length of dactyl about 0.65 that of propodus.

First pereopod extending to distal end of carpocerite or overreaching it by 0.5 length of dactyl. Second pereopod exceeding antennular peduncle by length of propodus or by latter and 0.15 that of carpus. Third pereopod overreaching antennular peduncle by propodus and about 0.5 length of carpus. Fourth pereopod surpassing antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth pereopod exceeding antennular peduncle by length of distal three podomeres. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and long slender spine on ischium; second pereopod with minute spine on basis. In female, coxa of third pereopod produced into large plate disposed at right angle to podomere, its anteromesial margin bearing blunt, strong tooth. Coxa of fourth pereopod produced in short, prominent plate armed with numerous strong setae. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, tooth considerably stronger in males than in females, in latter minute and borne on rounded coxal plate.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter somites with shallow median incision; sixth somite very elongate, 2.25 times as long as high, bearing small sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus, deep anteriorly, quite shallow posteriorly, and flanked by low sharp ridges; terminal portion length about 5 times basal width; lateral spines short, their length 1.5-1.6 times basal width of terminal portion of telson; mesial ramus of uropod falling short, or slightly overreaching, apex of telson; lateral ramus exceeding mesial ramus by 0.15-0.20 of its own length, and armed with acute, terminal, distolateral spine.

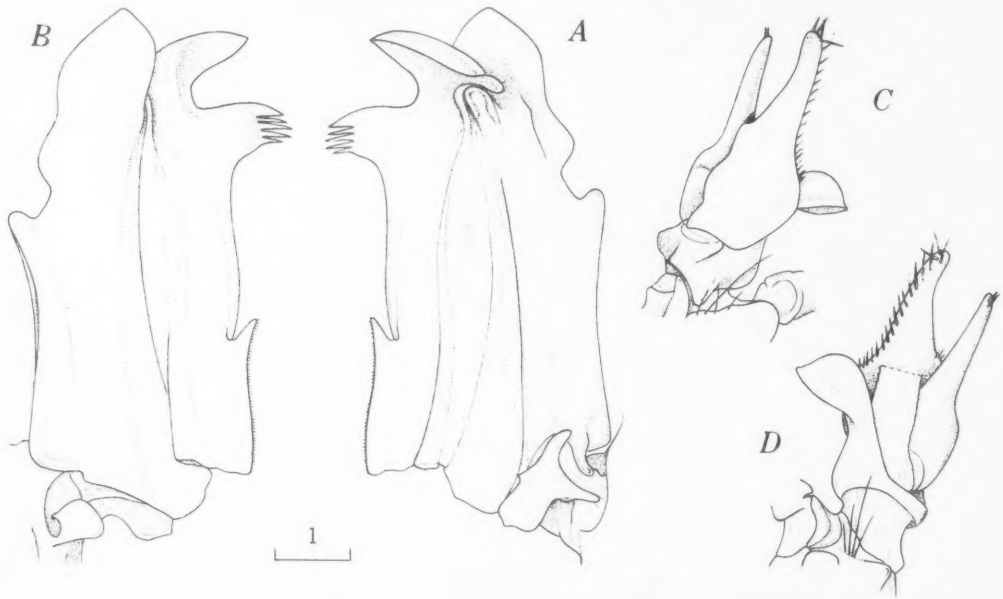

FIGURE 22.—*Hymenopenaeus nereus*, syntype ♂ 15.5 mm cl, northwest of Punta Galera, Ecuador. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventrolateral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

Petasma (Figure 22*A*, *B*) with row of cincinnuli occupying proximal 0.35 of median line; ventromedian lobule bearing two processes distally; mesial one (disposed almost at right angle to lobule) subrectangular, and armed with few long spines, distolateral one (directed at about 45 degrees to lobule) unarmed, and produced proximolaterally in small auricular process; distal flap of ventrolateral lobule acuminate, large, extending as far as lateral process, and almost straight rather than conspicuously inclined; ventral costa projecting in strong rounded prominence at base of flap.

Appendix masculina (Figure 22*C*, *D*) with proximal part produced into rounded lobe; distal part extremely narrow and bearing lateral row of short setae continuous with apical tuft of longer setae. Appendix interna abruptly narrowing, setting off distal part from rounded proximal part. Ventrolateral spur short, roughly semicircular in outline distally.

Thelycum (Figure 23) with median, longitudinal ridge on sternite XIV; lamella at posterior margin of sternite XIII rather flat, directed anteriorly, with distal (cephalic) margin slightly to deeply concave, and lateral margins convex basally, straight or concave distally; lamella flanked by pair of flattened, subtriangular to rounded processes directed caudally; posterior margin of sternite XII bearing paired, setose, long horns, reaching almost midlength of sternite XIII.

Maximum size.–Males: 18 mm cl; females: 27 mm cl.

Geographic and bathymetric ranges.–From south of Cabo Blanco (5°30′N, 86°45′W), Costa Rica, to northwest of Punta Galera and Islas Galápagos (00°36′S, 86°46′W), Ecuador (Figure 20). It has been found at depths between 1,271 and 3,279 m (Figure 9).

Affinities.–*Hymenopenaeus nereus* and *H. doris* are very similar in external morphology. However, the external genitalia allow a ready separation of these two species as well as both from the closely related *H. laevis* and *H. sewelli*. Females of *H. nereus* are unique among the four species in possessing a longitudinal ridge, instead of a large protuberance, on sternite XIV; furthermore, the median lamella of sternite XIII is directed anteriorly, its lateral margins tend to converge proximally (posteriorly), and the lamella is flanked by a pair of processes which are flattened and directed caudally. In the other species, these processes are lacking or, if present, are directed anteroventrally. Males of *H. nereus* differ from those of *H. laevis* in that the petasma of the latter bears two, occasionally three, small, triangular projections on the distomesial margin of the ventromedian lobule instead of a single, subrectangular process bearing spines distally. Moreover, the lateral process is small and extends transversely rather than being directed distomesially, and the distal part of the ventrolateral lobule is broadly semicircular and strongly inclined toward the ventromedian lobule.

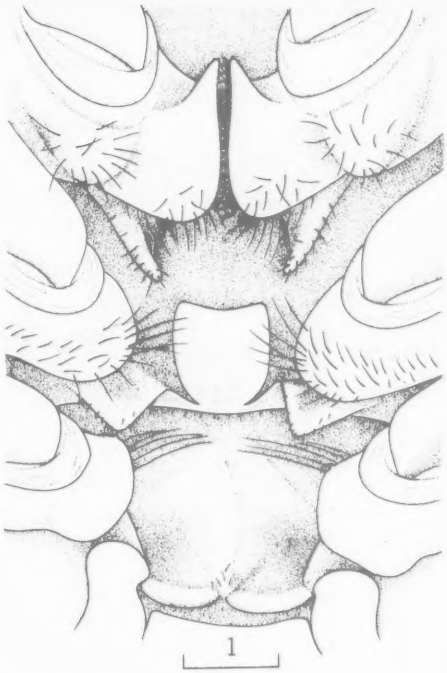

FIGURE 23.—*Hymenopenaeus nereus*, syntype ♀ 21.5 mm cl, south of Cabo Blanco, Costa Rica. Thelycum, ventral view.

Haliporoides Stebbing 1914

Peneopsis. Faxon 1893:212; 1895:185.

Faxonia Bouvier 1905a:981 [part, excluding type-species, *Penaeopsis ocularis* Faxon 1895 = *Pleoticus robustus* (Smith 1885)].

Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. de Man 1911:31 [part]. Calman 1925:9.

Haliporoides Stebbing 1914:20 [type-species, by monotypy, *Haliporoides triarthrus* Stebbing 1914. Gender, masculine]. Calman 1925:9.
Hymenopenaeus. Burkenroad 1936:102 [part].
Parahaliporus Kubo 1949:207.
Hymenopenaeus (Haliporoides). Barnard 1950: 619.

Diagnosis.–Body moderately robust, carapace elongate, integument firm. Rostrum relatively long, extending at least to, often beyond, second antennular article, ventral margin straight or concave; armed with dorsal and, frequently, with ventral teeth; epigastric tooth separated from rostral teeth by interval noticeably longer than spaces between latter. Orbital and branchiostegal spines absent; postorbital, antennal, pterygostomian, hepatic, and suprahepatic spines present. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus long, turning anteroventrally from almost horizontal posterior part and reaching base of pterygostomian spine; orbital-antennal and branchiocardiac carinae and sulci well marked; submarginal carina sharp. Abdomen carinate dorsally at least along three posterior somites. Telson with pair of fixed, lateral spines. Prosartema moderately long, broad, and flexible. Antennular flagella similar, subcylindrical and long, not less than 3 times carapace length. Mandibular palp three jointed (occasionally two jointed in *H. triarthrus,* Ivanov and Hassan 1976), proximal article short and narrow, intermediate one larger, scalene-triangular in shape, and distal article considerably shorter and narrower than preceding one and tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth pereopods relatively stout proximally, fifth not much longer than fourth. First pereopod with or without spine on basis. Exopods (quite small) on all maxillipeds and pereopods. Lateral ramus of uropod armed with subterminal, distolateral spine. In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal portion of rib of dorsolateral lobule not elevated above, but at level of adjacent area, and not projecting beyond distal margin; ventromedian lobule lacking paired processes distally; endopod of second pleopod bearing appendices masculina and interna, its basal sclerite produced into very short, toothlike, ventrolateral spur. Thelycum of open type. Pleurobranchia present on somites IX to XIV; single, rather conspicuous arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Eastern Pacific: *Haliporoides diomedeae* (Faxon 1893). Indo-West Pacific: *Haliporoides sibogae* (de Man 1907); *Haliporoides triarthrus* Stebbing 1914.

Affinities.–The members of *Haliporoides* can be distinguished readily from those belonging to other related genera by the following features: the epigastric tooth is separated from the series of rostral teeth by an interval conspicuously longer than the spaces between the latter; the presence of a suprahepatic spine and an orbitoantennal sulcus which, although shallow, is clearly distinct; the spine of the lateral ramus of the uropod which is subterminal. Also, the arthrobranchia on somite VII is well developed instead of being rudimentary and, in males, the basal sclerite of the second pleopod is produced into a very short, toothlike, rather than foliaceous, ventrolateral spur.

In addition to the characters cited above, *Haliporoides,* in contrast to *Hymenopenaeus,* possesses a thick, rigid integument, and lacks a branchiostegal spine and a posthepatic carina; it also possesses a petasma in which the ventromedian lobule is not produced distally into conspicuous processes, and the rib of the dorsolateral lobule is flush with the surrounding area. Finally, *Haliporoides* may be separated from *Pleoticus*–which it resembles in its general mien and in the shape of the rostrum—not only by the characters cited, but also by possessing a sharp branchiocardiac carina and deep branchiocardiac sulcus as well as by the petasma, in which the ventral costa is fused to the terminal part of the ventrolateral lobule. The above clearly indicates that *Haliporoides* is the most distinct of the genera treated here, except perhaps for *Mesopenaeus*.

Haliporoides diomedeae (Faxon 1893)

Figures 9, 20, 24-28

Peneopsis diomedeae Faxon 1893:212 [syntypes: 3 ♀, USNM 21175, off Golfo de Panamá, 7°31′30″N, 79°14′00″W, 458 fm (838 m), 8 March

1891, *Albatross* stn 3384. 1 ♂ 1 ♀, USNM 21176, SW of Golfo de Panamá, 7°30′36″N, 78°39′00″W, 730 fm (1,335 m), 11 March 1891, *Albatross* stn 3395. 2 ♂ 1 ♀, MCZ 4644, SE of Golfo de Panamá, 7°21′N, 79°35′W, 511 fm (935 m), 10 March 1891, *Albatross* stn 3394. 3 ♀, off Punta Mala, Panama, 7°15′N, 79°36′W, 1,020 fm (1,866 m), 10 March 1891, *Albatross* stn 3393. 2 ♀, off Punta Mariato, Panama, 7°06′15″N, 80°34′00″W, 695 fm (1,271 m), 23 February 1891, *Albatross* stn 3353. 1 ♂, USNM 21174, S of Península de Azuero, 6°30′N, 81°44′W, 555 fm (1,015 m), 24 February 1891, *Albatross* stn 3358]. Faxon 1895:185, pl. G.

Faxonia diomedeae. Bouvier 1905a:981.

Haliporus diomedeus. Bouvier 1906b:4; 1908:80.

Haliporus diomedeae. de Man 1911:7.

Hymenopenaeus diomedeae. Burkenroad 1936: 104. Hancock and Henríquez 1968:445. Idyll 1969:641. Chirichigno Fonseca 1970:13, fig. 18. del Solar C. et al. 1970:18. Arana Espina and Cristi V. 1971:25. Illanes B. and Zúñiga C. 1972: 3, pl. 1-2.

Hymenopenaeus diomedaea. Bahamonde 1963:3 (unnumbered).

Vernacular names; gamba roja (Peru); gamba, camarón de mar, camarón de profundidad (Chile).

Material

PANAMA—2 ♀, MCIP, 32 km SE of Punta Mala, Península de Azuero, 823-1,006 m, 1973, *Canopus*. 3 ♀ syntypes, USNM 21175, off Golfo de Panamá, 458 fm (838 m), 8 March 1891, *Albatross* stn 3384. 1 ♂ 1 ♀ syntypes, USNM 21176, SW of Golfo de Panamá, 730 fm (1,335 m), 11 March 1891, *Albatross* stn 3395. 2 ♂ 1 ♀ syntypes, MCZ 4644, SE of Golfo de Panamá, 511 fm (935 m), 10 March 1891, *Albatross* stn 3394. 1 ♂ syntype, USNM 21174, S of Península de Azuero, 555 fm (1,015 m), 24 February 1891, *Albatross* stn 3358.

PERU—1 ♀, USNM, off Casitas, Tumbes, 550 m, 16 December 1968, *Kaiyo Maru*. 58 ♂ 56 ♀, USNM, W of I Macabí, 607-735 m, 5 September 1966, *Anton Bruun* stn 754.

CHILE—4 ♀, USNM, off Paposo, Antofagasta, 950 m, 16 August 1966, *Anton Bruun* stn 714. 8 ♂ 13 ♀, USNM, off Bahía Pichidangui, Coquimbo, 960 m, 12 August 1966, *Anton Bruun* stn 703. 1 ♂ 1 ♀, USNM, Valparaíso, 10 February 1956, John Manning. 14 ♂ 17 ♀, USNM, off Punta Topocalma, Colchagua, 750-730 m, 5 August 1966, *Anton Bruun* stn 687.

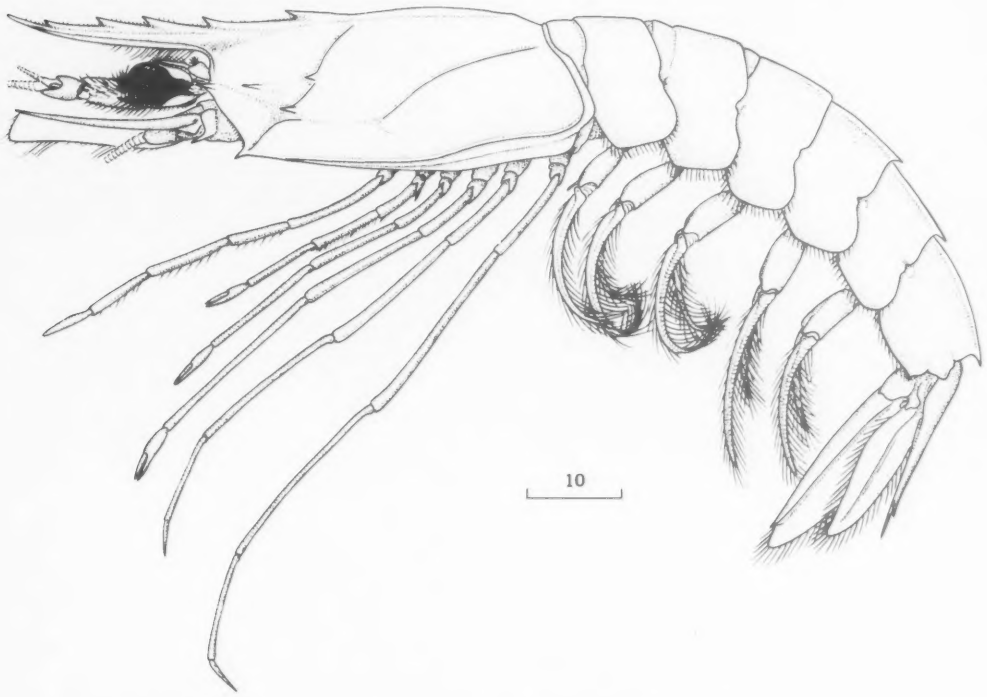

FIGURE 24.—*Haliporoides diomedeae*, ♀ 37.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. Lateral view.

Description.–Body rather robust (Figure 24), integument firm and glabrous. Rostrum straight or gently sinuous with upturned tip, moderately long, at most slightly overreaching antennular peduncle, its length 0.45-0.60 that of carapace. Rostral plus epigastric teeth 3-6 (mode 5; N = 100); epigastric tooth situated at about 0.3 length of carapace from orbital margin, first rostral at level of, or immediately posterior to, orbital margin. Adrostral carina strong, extending from orbital margin almost to apex of rostrum; postrostral carina very strong to near posterior margin of carapace, there merging with inconspicuous dorsal tubercle. Antennal, pterygostomian, postorbital, and hepatic spines long, slender, and sharp; both antennal and postorbital spines (latter situated directly posterior to antennal) continuous with short, blunt, basal carina; basally broad suprahepatic spine (occasionally accompanied by smaller dorsal one) present, giving rise to deep notch dorsal to hepatic spine; orbitoantennal sulcus shallow, but clearly distinct; cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located almost 0.45 length of carapace from orbital margin; hepatic sulcus deep, hepatic carina sharp anteriorly and turning anteroventrally to base of pterygostomian spine; both hepatic carina and sulcus almost indistinct posteriorly, to anteroventral end of branchiocardiac sulcus. Branchiocardiac carina long, sinuous, and sharp, accompanying sulcus deep and broad; submarginal carina long, extending from base of pterygostomian spine to posterior margin of carapace.

Eye (Figure 25) with basal article produced distomesially into pubescent, relatively short scale; ocular peduncle short, bearing rather small mesial tubercle; cornea subreniform, greatest diameter about 2 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema broad and short, extending only to distomesial extremity of ocular peduncle; stylocerite extending about 0.6 of distance between its proximal extremity and mesial base of distolateral spine; latter moderately long, slender, and sharp. Antennular flagella long, although incomplete in all specimens examined, in shrimp 32.5 mm cl, broken dorsal flagellum 118 mm long, thus 3.65 times as long as carapace. Scaphocerite overreaching antennular peduncle by about 0.2 of its own length;

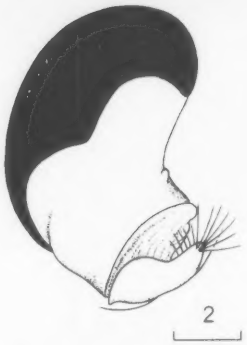

FIGURE 25.—*Haliporoides diomedeae*, ♀ 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Eye.

lateral rib ending in rather slender spine, falling short of distal margin of lamella. Antennal flagellum broken in specimens examined, according to Illanes and Zúñiga (1972) "longer than total length of body."

Mandibular palp (Figure 26*A*) extending as far as basal 0.4 length of carpocerite; proximal article scalene-triangular, about 2.65 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae as illustrated (Figure 26*B, C*); somite VII bearing single conspicuous arthrobranchia at base of first maxilliped (Figure 26*De-e*[1]). Third maxilliped reaching beyond antennular peduncle by tip or by length of dactyl in males and by as much as dactyl and 0.5 length of propodus in females; dactyl with acute tip in females, clublike in males, its length 0.90-0.95 that of propodus.

First pereopod reaching between base and distal end of carpocerite in males, and almost to distal end of carpocerite or overreaching it by as much as length of dactyl in females. Second pereopod extending, at most, to midlength of second antennular article in males, and as far as distal end of third article in females. Third pereopod reaching distal end of third antennular article or overreaching it by not more than length of dactyl in males, and by entire propodus plus 0.15 length of carpus in large females. Fourth pereopod exceeding antennular peduncle by, at most, length of dactyl in males, and by dactyl or by entire propodus in females. Fifth pereopod overreaching antennular peduncle by as much as length of dactyl and 0.8 that of propodus in males, and by distal two podomeres plus 0.15-0.25 length

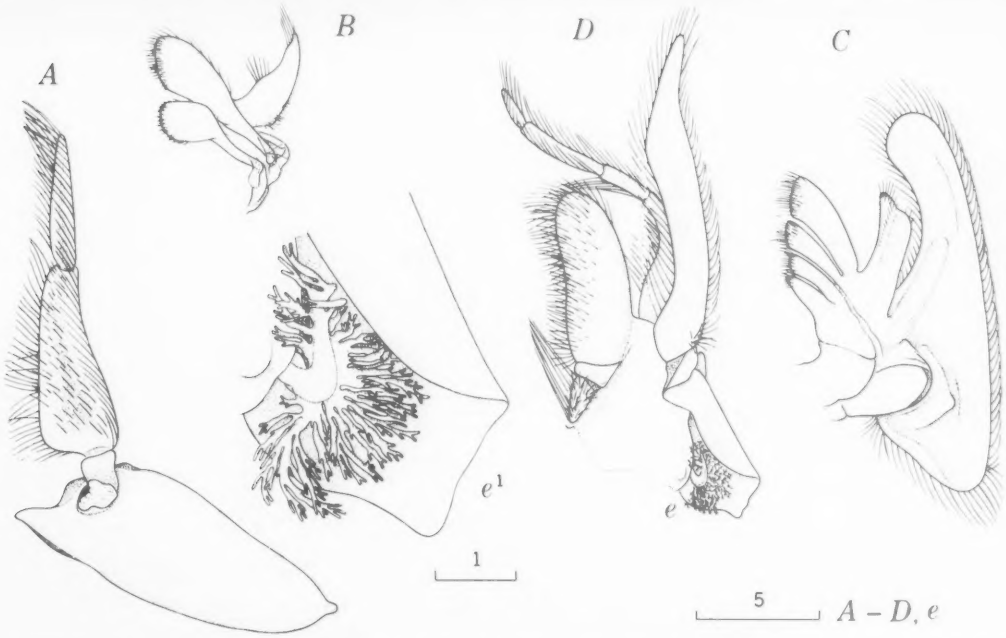

FIGURE 26.—*Haliporoides diomedeae*, ♀ 45.5 mm cl, Valparaíso, Chile. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *e*, Arthrobranchia. e^1, Enlargement of *e* (all from left side).

of carpus in females. Pereopods increasing in length from first to fifth; third and fourth extending distally for about same distance. First pereopod with spine on basis and ischium, and one movable distal spine and one or two fixed proximal ones on merus; basis of second pereopod lacking spine. In females, coxal plate of third pereopod directed and broadening mesially, strongly convex posteriorly. In both sexes, anteromesial spine present on coxae of third through fifth pereopods; in females, spine on third long, slender, and situated anterodorsally to coxal plate, and spines on fourth and fifth small and sharp; in males, spines on third and fourth pereopods small and sharp, but spine on fifth large, flattened, curved laterally.

Abdomen with middorsal keel from fourth through sixth somites and strong, sharp spine at posterior end of keel on each; sixth somite short, about 1.25 times as long as high, bearing posteroventral spines. Telson with broad median sulcus deep anteriorly, shallower posteriorly, ending at level of base of lateral spines, and flanked by well-defined ridges; terminal portion length 4-5 times basal width, spines short, 1.0-1.65 times basal width of terminal portion. Mesial ramus of uropod reaching apex of telson or overreaching it by about 0.15 of its own length; lateral ramus, in turn, overreaching mesial by almost 0.2 of its own length, armed with rather strong, subterminal, distolateral spine. Third through fifth pleopods in males bearing strong dorsomesial ridge, that of third bearing distally strong subrectangular tooth with minute tooth at its base; ridge on fourth ending in also large, subtriangular tooth; last three pleopods in females with barely marked dorsomesial ridge.

Petasma (Figure 27*A*, *B*) with row of cincinnuli occupying only proximal 0.3 of median line; terminal part of ventromedian lobule abruptly broadening distally with terminal margin serrate laterally; rib of dorsolateral lobule broad proximally, its distal extremity reaching, but not overreaching, margin of adjacent membranous portion; distal part of ventrolateral lobule free, forming roughly subelliptical flap diverging from ventromedian lobule; ventral costa broad proximally, tapering along margin of flap.

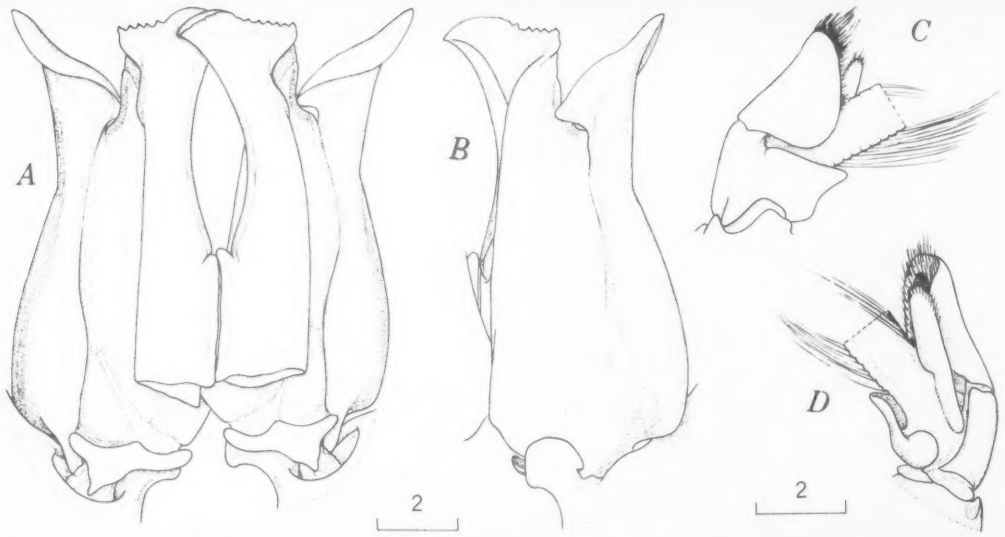

FIGURE 27.—*Haliporoides diomedeae*, ♂ 34.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. *A*, Petasma, dorsal view (partly bent laterally). *B*, Ventral view of left half. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

Appendix masculina (Figure 27*C*, *D*) short, length about 1.5 times maximum width, produced laterally into broad semicircular lobe, ventrally excavated and bearing patch of long setae along entire distal margin. Appendix interna falling short of distal margin of appendix masculina, and armed with thickly set setae along entire distal margin; distolateral spur very short and obtuse.

Thelycum (Figure 28) with no ridge or protuberance on sternite XIV, latter smoothly convex or low subconical, often bearing minute central tubercle; posterior part of sternite XIII armed with strong median, acute to blunt subconical protuberance directed anteriorly and studded with numerous setae on anterior half; posterior margin of sternite XII lacking horns.

Color.–Overall pink with red and orange patches and bands, both longitudinal and transverse. For detailed account of coloration see Illanes B. and Zúñiga C. (1972).

Maximum size.–Males: 50 mm cl; females: 57 mm cl (in material examined by me).

Geographic and bathymetric ranges.–Off Península de Azuero, Panama (Figure 20) to Talcahuano, Chile (36°40′S), in depths between 240 (Illanes B. and Zúñiga C. 1972) and 1,866 m (Figure 9). Information on the geographic and bathymetric distributions of this species, as well as of its other two congeners in the American Pacific, is extremely meager.

Affinities.–Haliporoides diomedeae is the only member of the genus occurring in American waters and may thus be readily distinguished from the other solenocerids in the region by generic characters. Its two congeners, the Indo-West Pacific *H. sibogae* and *H. triarthrus*, differ from it in possessing an arcuate, ventrally toothed rostrum, and in lacking meral spines on the first pair of pereopods, as well as in petasmal and thelycal features. In both of them, the ventromedian lobule of the petasma is neither expanded distally nor serrate along its terminal margin, and the thelycum exhibits a midridge on sternite XIII instead of a subconical, median protuberance.

Remarks.–Studies of this species are extremely few, and almost entirely restricted to its external morphology. The most recent contribution is one by Illanes B. and Zúñiga C. (1972), who presented many fine observations on numerous features. Previously, Arana Espina and Cristi V. (1971) had determined the relations between the following parameters: carapace length, total length,

whole weight, and abdominal weight (cl/tl, cl/ww, cl/aw, tl/ww, tl/aw). They found statistically significant differences between males and females in all relations with the exception of carapace length/total length.

Economic importance.–At present this species is not taken commercially. However, dense concentrations have been located in various areas within its range. Off the west coast of America three deepwater shrimps—*Solenocera agassizii* Faxon 1893; *Solenocera florea* Burkenroad 1938, and *Heterocarpus reedi* Bahamonde 1955—are utilized; consequently, it is to be expected that *H. diomedeae,* a species larger than those mentioned above, eventually will be exploited.

Pleoticus Bate 1888

Philonicus Bate 1888:273 [part, excluding *Philonicus lucasii* (Bate 1881) = *Hadropenaeus lucasii,* and *Philonicus pectinatus* Bate 1888 = *Solenocera pectinata*]. [Type-species, by subsequent designation of Fowler 1912:543, *Philonicus mülleri* Bate 1888]. Preoccupied by *Philonicus* Loew 1849:144 (Diptera).

Pleoticus Bate 1888:xii [part]. [Replacement name for *Philonicus* Bate. Type-species, *Philonicus mülleri* Bate 1888. Gender, masculine].

Faxonia Bouvier 1905a:981 [part, excluding *Faxonia diomedeae* (Faxon 1893)]. [Type-species, by subsequent designation of Fowler 1912:543, *Penaeopsis ocularis* Faxon 1895 = *Pleoticus robustus* (Smith 1885)].

Parartemesia Bouvier 1905b:747 [part, excluding *Parartemesia tropicalis* Bouvier 1905b = *Mesopenaeus tropicalis* (Bouvier 1905b)]. [Type-species, by subsequent designation of Fowler 1912:543, *Parartemesia carinata* Bouvier 1905b = *Pleoticus muelleri* (Bate 1888)].

Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part]. Fowler 1912:542 [part].

Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part]. Roberts and Pequegnat 1970:29 [part].

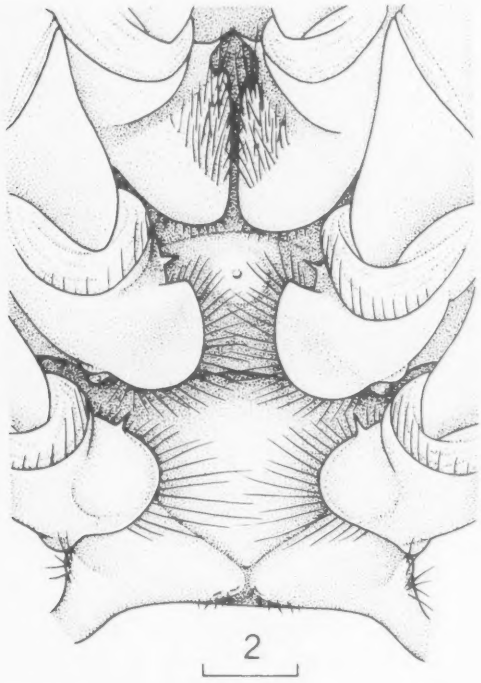

FIGURE 28.—*Haliporoides diomedeae,* ♀ 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Thelycum, ventral view.

Diagnosis.–Body robust, carapace elongate, integument thick, firm. Rostrum moderately long, reaching midlength of second antennular article or slightly overreaching peduncle; ventral margin straight to concave; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than, that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian spine absent; branchiostegal spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; posthepatic and branchiocardiac carina lacking; branchiocardiac sulcus usually absent; submarginal carina sharp; posthepatic carina absent. Abdomen carinate dorsally at least along posterior three somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long or moderately long, flexible. Antennular flagella similar, subcylindrical, and longer than carapace. Mandibular palp two jointed, articles broad, distal one as long, or almost as long, as basal, tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth pereopods rather stout proximally, fifth moderately longer than fourth. First pereopod with spine on basis and ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of

uropod armed with terminal, distolateral spine. In males, petasma with ventral costa free from distally flexible terminal part of ventrolateral lobule; ventromedian lobule not expanded distally. Endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; one or two rudimentary arthrobranchiae on somite VII; and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.–Western Atlantic: *Pleoticus robustus* (Smith 1885); *Pleoticus muelleri* (Bate 1888). Red Sea: *Pleoticus steindachneri* (Balss 1914).

Affinities.–The members of *Pleoticus* resemble those of *Hymenopenaeus* and *Haliporoides* in the character of the rostrum and general form of the carapace; however, in *Pleoticus* the epigastric tooth is separated from the first rostral by an interval which is equal to, or only slightly greater than, that between the first and second rostral teeth; an orbital spine is present as it only is in the more distantly related *Mesopenaeus;* the branchiocardiac carina is absent; and the branchiocardiac sulcus is usually absent. Furthermore, the mandibular palp is two jointed unlike the usually three jointed one of *Haliporoides* but like that of *Hymenopenaeus;* however, in contrast to the palp of the latter, that of *Pleoticus* is broad and its distal article is as long as, or longer than, the basal. Finally, in the petasma of *Pleoticus* the distal extremity of the ventral costa is free from the ventrolateral lobule instead of being fused to it.

Pleoticus agrees with *Hadropenaeus* in the arrangement of the epigastric and rostral series of teeth, the lack of branchiocardiac and posthepatic carinae, the absence of pterygostomian spines, as well as in having the distal extremity of the ventral costa of the petasma free from the adjacent part of the ventrolateral lobule. The considerably more elongate carapace, the low and longer rostrum, and the presence of strong submarginal carina, and orbital spine separate the former from the latter.

The similarities cited above indicate that *Pleoticus* occupies a position somewhat intermediate between the more primitive *Hymenopenaeus* and *Haliporoides,* on one hand, and *Hadropenaeus* on the other.

The genus *Pleoticus* is less homogeneous than the other genera treated here. In *P. robustus* and *P. muelleri* the branchiocardiac sulcus is abent or indistinct whereas in *P. steindachneri* it is distinctly marked; the branchiostegal spine, while present in *P. robustus* and *P. muelleri,* is lacking in *P. steindachneri.* Whereas in the petasma of *P. robustus* and *P. steindachneri* the row of cincinnuli occupies almost the entire median line, and the ventromedian lobule is distally membranous and entire, in that of *P. muelleri* the row of cincinnuli is limited to the proximal 0.4 of the median line, and the ventromedian lobule is heavily sclerotized distally and bears strong projections. In spite of these differences, it seems to me that the many features shared by these species justify their being grouped within a single genus. I have not examined specimens of *P. steindachneri,* but the descriptions and illustrations of Balss (1914, 1915) indicate that this shrimp is more closely related to *P. robustus* and *P. muelleri* than to members of other genera.

Key to the Species of *Pleoticus* in the western Atlantic

1. Body entirely pubescent. Prosartema not overreaching distal margin of first antennular article. Branchiostegal spine present. Females with paired, triangular projections near anterior margin of sternite XIV, and strong median ridge on sternite XIII. Males with petasma cincinnulate along entire median line, its ventromedian lobule entire distally ..... *P. robustus*

   Body almost entirely polished. Prosartema considerably overreaching distal margin of first antennular article. Branchiostegal spine absent. Females lacking triangular projections on sternite XIV, bearing strong, median projection on sternite XIII. Males with petasma cincinnulate along proximal 0.4 of median line, its ventromedian lobule produced in two projections .... *P. muelleri*

Pleoticus robustus (Smith 1885)

Figures 9, 29-36

Hymenopenaeus robustus Smith 1885:180 [syntypes: 2 ♂ 7 ♀, USNM 6907; 2 ♂ 5 ♀ (1 ♀ in original lot = *Penaeopsis serrata* Bate 1881), USNM 6908; type-locality: 11°43′00″N, 69°09′30″W, 208 fm (380 m), S of Curaçao, *Albatross* stn 2125]. Burkenroad 1936:118. Anderson and Lindner 1945:288. U.S. Fish and Wildlife Service 1948:2. Springer 1951a:80; 1951b: 6. Springer and Bullis 1952:11. Popovici and Angelescu 1954:509. Springer and Bullis 1954: 3. Voss 1955:9, fig. 6. Bullis 1956:1 [not Fig. 1 = *Aristeus antillensis* A. Milne Edwards and Bouvier 1909]. Springer and Bullis 1956:8. Clifford 1956:438. Guest 1956:7. Lindner 1957:87. Anderson 1958:1, fig. 6. U.S. Fish and Wildlife Service 1958:1, fig. I-6. Bullis and Thompson 1959a:35; 1959b:1. Hutton et al. 1959:7. Eldred and Hutton 1960:91, fig. 12. Cummins and Rivers 1962:19. Bullis and Cummins 1963:9. Davant 1963:21, fig. 19-20. Boschi 1964:38. Hutton 1964:439. Bullis and Thompson 1965:5. Holthuis and Rosa 1965:1. Pericchi López 1965: 24. Joyce and Eldred 1966:24. Kutkuhn 1966: 21. Christmas and Gunter 1967:1442. Thompson 1967:1454. Idyll 1969:638. Klima 1969:1. Roe 1969:161, fig. 1. Anderson and Bullis 1970: 112. Pérez Farfante 1970:13, fig. 3F-H. Roberts and Pequegnat 1970:30, fig. 3-1B-C. Anderson and Lindner 1971:313, fig. 1-7. García Pinto 1971:5. Pequegnat and Roberts 1971:8. García del Barco 1972:172.

Peneopsis ocularis Faxon 1895:187.

Faxonia ocularis. Bouvier 1905a:981.

Haliporus robustus. Bouvier 1906b:4; 1908:8. A. Milne Edwards and Bouvier 1909:210, fig. 29-37, pl. 1, fig. 14-15, pl. 2, fig. 1-7. de Man 1911:7. Lenz and Strunck 1914:303. Burkenroad 1934:69.

Parapenaeus paradoxus Boone 1927:79 [part].

Hymenopeneus robustus. Burkenroad 1963a:173.

Royal red shrimp. Bates 1957:9, figures. Bullis and Rathjen 1959:1. Anonymous 1977:2.

Vernacular names: royal red shrimp (United States), camarón rojo gigante (Mexico), camarón real rojo (Cuba), langostino rojo (Venezuela).

Material

UNITED STATES—Massachusetts: 2 ♂ 2 ♀, USNM, S of Martha's Vineyard, 320 m, 28 January 1960, *Delaware* stn 39. 1 ♀, USNM, off Georges Bank, 20 July 1955, *Delaware*. North Carolina: 1 ♂ 1 ♀, USNM, NE of Cape Lookout, 348-384 m, 13 November 1956, *Combat* stn 171. 6 ♀, USNM, off Cape Lookout, 366 m, 22 June 1957, *Combat*

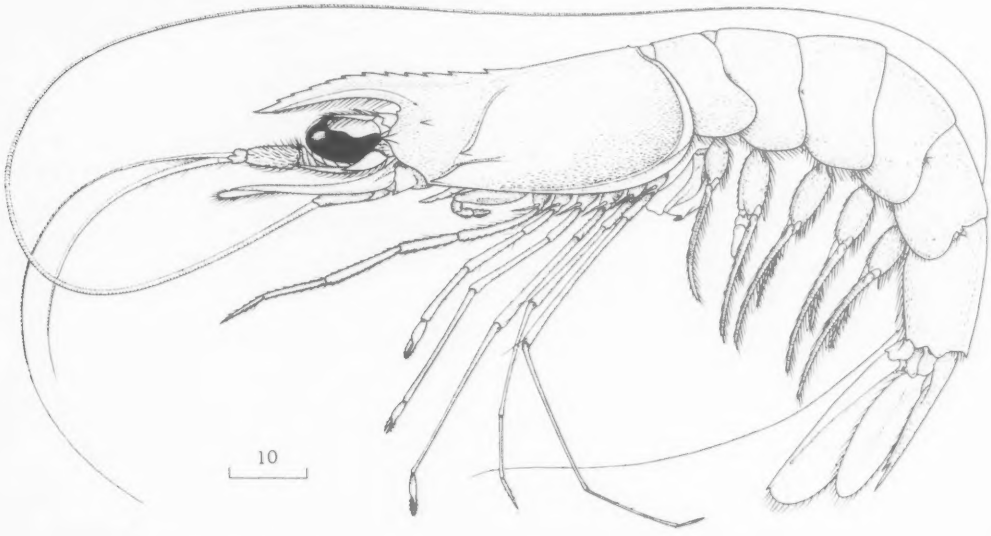

FIGURE 29.—*Pleoticus robustus*, ♂ 31 mm cl, east of Península Valiente, Panama. Lateral view.

stn 410. 5 ♂ 5 ♀, USNM, SE of Cape Fear, 402 m, 29 January 1972, *Oregon II* stn 11746. South Carolina: 1 ♂ 1 ♀, USNM, off Port Royal Sound, 366 m, 23 January 1972, *Oregon II* stn 11734. Florida: 3 ♂, USNM, off St Augustine, 384-393 m, 9 February 1965, *Oregon* stn 5231. 1 ♂ 3 ♀, USNM, off St Augustine, 344-338 m, 1 May 1956, *Pelican* stn 41. 3 ♀, USNM, off St Augustine, 316-329 m, 2 May 1956, *Pelican* stn 46. 1 ♂ 22 ♀, USNM, off St Augustine, 324-333 m, 3 February 1962, *Silver Bay* stn 3725. 28 ♂ 30 ♀, USNM, off Flagler Beach, 384 m, 16 November 1964, *Oregon* stn 5107. 1 ♂ 2 ♀, USNM, off Coronada Beach, 348 m, 10 February 1965, *Oregon* stn 5241. 9 ♂ 6 ♀, USNM, off Oak Hill, 402-430 m, 11 February 1965, *Oregon* stn 5247. 4 ♀, USNM, off Cape Kennedy, 338 m, 27 January 1962, *Silver Bay* stn 3714. 5 ♂ 6 ♀, USNM, off Cocoa Beach, 329 m, 11 March 1956, *Pelican* stn 13. 11 ♂ 15 ♀, RMNH, E of Hutchinsons I, 324 m, 16 July 1965, *Gerda* stn 654. 11 ♂ 13 ♀, UMML, off St Lucie Inlet, 366-375 m, 21 May 1968, *Gerda* stn 998. 15 ♂ 14 ♀, USNM, SE of St Lucie Inlet, 287-262 m, 16 July 1965, *Gerda* stn 655. 2 ♂, USNM, E of Carysfort Reef, 549 m, 23 July 1957, *Combat* stn 444. 1 ♂ 1 ♀, USNM, off Islamorada, 457-476 m, 18 July 1955, *Oregon* stn 1351. 3 ♂ 2 ♀, USNM, off Double Headed Shot Cays, 558-514 m, 29 August 1967, *Gerda* stn 861. 1 ♀, UMML, S of Marquesas Keys, 512 m, 2 February 1968, *Gerda* stn 970. 9 ♀, USNM, SW of Marquesas Keys, 402-267 m, 2 February 1968, *Gerda* stn 969. 6 ♂ 4 ♀, USNM, SW of Marquesas Keys, 437-320 m, 2 February 1968, *Gerda* stn 968. 1 ♀, UMML, S of Dry Tortugas, 622 m, 28 April 1969, *Gerda* stn 1099. 2 ♂ 3 ♀, UMML, S of Dry Tortugas, 459-494 m, 28 April 1969, *Gerda* stn 1098. 26 ♂ 27 ♀, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 5 ♂ 8 ♀, USNM, SW of Dry Tortugas, 402 m, 15 June 1956, *Oregon* stn 1539. 1 ♂, USNM, NW of Dry Tortugas, 311-366 m, 7 July 1955, *Oregon* stn 1321. 2 ♂ 2 ♀, USNM, S of St George I, 366 m, 21 August 1970, *Oregon II* stn 11180. 2 ♂ 2 ♀, USNM, S of Santa Rosa I, 439 m, 28 August 1970, *Oregon II* stn 11189. 1 ♀, USNM, S of Santa Rosa I, 527 m, 4 February 1970, *Oregon II* stn 10899. 9 ♂ 6 ♀, USNM, off Gulf Beach, 576-622 m, 28 April 1951, *Oregon* stn 319. Alabama (all from off Mobile Bay): 4 ♀, USNM, 549 m, 10 August 1970, *Oregon II* stn 11137. 1 ♀, USNM, 594 m, 10 August 1970, *Oregon II* stn 11139. 2 ♂ 2 ♀, USNM, 433 m, 22 June 1969, *Oregon II* stn 10640. 1 ♂ 4 ♀, USNM, 366 m, 18 December 1962, *Oregon* stn 4151. 8 ♀ juv, YPM, 219-238 m, 24 March 1935, *Atlantis* stn 2377. 3 ♀, USNM, 512 m, 10 July 1952, *Oregon* stn 597. Louisiana: 1 ♂, AMNH, E of Mississippi Delta, 384 m, 11 February 1885, *Albatross* stn 2377. 1 ♂, USNM, E of Mississippi Delta, 357 m, 1 September 1970, *Oregon II* stn 11202. 4 ♀, USNM, E of Mississippi Delta, 549 m, 23 October 1962, *Oregon* stn 4005. 14 ♂ 9 ♀, USNM, E of Mississippi Delta, 357 m, 23 September 1950, *Oregon* stn 126. 7 ♂ 10 ♀, USNM, E of Mississippi Delta, 402 m, 22 April 1951, *Oregon* stn 307. 3 ♂ 17 ♀, USNM, E of Mississippi Delta, 402 m, 25 August 1962, *Oregon* stn 3733. 1 ♀, YPM, E of Mississippi Delta, 302 m, 26 March 1935, *Atlantis* stn 2381. 3 ♂, USNM, off Atchafalaya Bay, 402 m, 11 November 1951, *Oregon* stn 501. Texas: 2 ♂ 3 ♀, USNM, SSE of Galveston, 366 m, 18 November 1951, *Oregon* stn 503. 3 ♂ 4 ♀ 2 juv, USNM, E of St Joseph I, 503 m, 6 May 1956, *Oregon* stn 1506. 1 ♂, USNM, off Corpus Christi, 640-732 m, 16 April 1952, *Oregon* stn 543. 1 ♂ 2 ♀, USNM, off Padre I, 549 m, 23 January 1964, *Oregon* stn 4637. 1 ♂ juv, USNM, off Port Isabel, 640 m, 6 August 1969, *Western Gulf* stn 38. 1 ♀, USNM, off Brownsville, 457 m, 6 August 1969, *Western Gulf* stn 39.

MEXICO—Tamaulipas: 1 ♂ 1 ♀, USNM, off Las Lavaderos, 558 m, 2 June 1970, *Oregon II* stn 10953. 2 ♀, USNM, off Las Lavaderos, 677 m, 2 June 1970, *Oregon II* stn 10954. Veracruz: 2 ♂ 2 ♀, USNM, N of Punta Roca Partida, 357 m, 5 June 1970, *Oregon II* stn 10959. 1 ♂ 1 ♀, USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, *Oregon II* stn 10960. Tabasco: 1 ♀, USNM, NW of Laguna del Carmen, 430 m, 6 June 1970, *Oregon II* stn 10963. 1 ♀, USNM, N of Punta Frontera, 613 m, 9 June 1970, *Oregon II* stn 10984.

HAITI—14 ♂ 7 ♀, USNM, off Cape-Haitien, 640 m, 12 February 1963, *Silver Bay* stn 5142.

DOMINICAN REPUBLIC—1 ♂ 1 ♀, USNM, E of Puerto Plata, 732-640 m, 15 October 1963, *Silver Bay* stn 5168.

LESSER ANTILLES—4 ♀, USNM, off Dog I, 628 m, 6 December 1969, *Oregon II* stn 10835. 2 ♀, USNM, off Dog I, 688 m, 6 December 1969, *Oregon II* stn 10834. 7 ♂ 6 ♀, USNM, NE of Saba I, 649-668 m, 18 May 1967, *Oregon* stn 6696. 4 ♂ 5 ♀, USNM, E of Sint Eustatius, 642 m, 8 December 1969, *Oregon II* stn 10840. 2 ♂ 6 ♀, USNM, E of St Christopher, 644 m, 8 December 1969, *Oregon II* stn 10841. 34 ♂ 31 ♀, USNM, off St Christopher, 640-676 m, 20 May 1967, *Oregon* stn 6701. 2 ♀, USNM, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, *Pillsbury* stn 936. 2 ♂ 7 ♀ syntypes, USNM 6907, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 2 ♂ 5 ♀ syntypes, USNM 6908, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 1 ♀, USNM, NW of Aruba, 622 m, 26 November 1970, *Oregon II* stn 11307.

WESTERN CARIBBEAN—2 ♂ 1 ♀, USNM, W of Rosalind Bank, 366 m, 7 June 1962, *Oregon* stn 3627. 2 ♂ 1 ♀, USNM, NE of Cayos Hobbies, 521 m, 25 October 1970, *Oregon II* stn 11220. 3 ♀, USNM, W of Rosalind Bank, 457 m, 24 August 1957, *Oregon* stn 1889. 32 ♂ 26 ♀, UMML, W of Quita Sueño Bank, 450-576 m, 31 January 1971, *Pillsbury* stn 1355. 5 ♂ 2 ♀, USNM, W of Quita Sueño Bank, 439-457 m, 21 May 1962, *Oregon* stn 3565. 1 ♀, USNM, SW of I de Providencia, 549 m, 13 September 1957, *Oregon* stn 1927. 1 ♂ 2 ♀, USNM, W of I de San Andrés, 549 m, 27 October 1970, *Oregon II* stn 11225. 1 ♀, USNM, W of Cayos de Albuquerque, 585 m, 27 October 1970, *Oregon II* stn 11226. 1 ♀, USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, *Oregon* stn 6444.

MEXICO—Quintana Roo: 1 ♂ 5 ♀, USNM, off I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BELIZE—8 ♂ 2 ♀, YPM, off Glover Reef, 669 m, 29 April 1925, *Pawnee*. 4 ♂ 6 ♀, USNM, off Stann Creek, 457-732 m, 10 June 1962, *Oregon* stn 3635. 2 ♂ 3 ♀, USNM, off Jonathan Point, 348 m, 9 June 1962, *Oregon* stn 3643.

NICARAGUA—2 ♂ 2 ♀, USNM, NE of Islas del Maíz, 549-585 m, 23 May 1962, *Oregon* stn 3576.

PANAMA—8 ♂ 14 ♀, USNM, E of Península Valiente, 512 m, 25 May 1962, *Oregon* stn 3583. 6 ♂ 9 ♀, USNM, Golfo de los Mosquitos, 549 m, 31 May 1962, *Oregon* stn 3600. 1 ♂ 3 ♀, USNM, Golfo de los Mosquitos, 732 m, 31 May 1962, *Oregon* stn 3601. 2 ♀, USNM, NE of Belén, 439 m, 30 May 1962, *Oregon* stn 3592. 1 juv, USNM, off Punta Manzanillo, 421 m, 19 October 1965, *Oregon* stn 5740. 1 ♂, USNM, 5 July 1972, *Canopus*.

COLOMBIA—1 ♀, USNM, off Punta Broquelles, 732 m, 28 May 1964, *Oregon* stn 4902. 3 ♂ 3 ♀, USNM, N of Islas de San Bernardo, 549 m, 6 November 1970, *Oregon II* stn 11244. 7 ♂ 8 ♀, USNM, off Puerto Colombia, 366 m, 2 December 1968, *Oregon II* stn 10260. 4 ♀, USNM, W of Santa Marta, 631 m, 9 November 1970, *Oregon II* stn 11250. 1 ♂ 1 ♀, USNM, W of Ríohacha, 567-531 m, 30 July 1968, *Pillsbury* stn 781. 6 ♂ 3 ♀, UMML, W of Cabo de la Vela, 408-576 m, 29 July 1968, *Pillsbury* stn 776. 3 ♂ 7 ♀, USNM, W of Cabo de la Vela, 366 m,

2 June 1964, *Oregon* stn 4922. 21 ♂ 15 ♀, USNM, W of Cabo de la Vela, 439-448 m, 2 June 1964, *Oregon* stn 4923. 3 ♂ 2 ♀, USNM, off Cabo de la Vela, 485 m, 9 October 1965, *Oregon* stn 5689.

VENEZUELA—8 ♀, USNM, E of Península de Paraguaná, 421 m, 27 September 1963, *Oregon* stn 4406. 4 ♀, USNM, off Península de Paraguaná, 457 m, 4 October 1963, *Oregon* stn 4419. 4 ♀, USNM, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 3 ♂ 9 ♀, USNM, off Península de Araya, 402 m, 20 October 1963, *Oregon* stn 4477. 2 ♂ 9 ♀, USNM, NE of Islas Los Testigos, 366-439 m, 24 September 1964, *Oregon* stn 5037. 10 ♂ 11 ♀, USNM, NE of Islas Los Testigos, 388-457 m, 23 September 1958, *Oregon* stn 2353. 5 ♂ 6 ♀, USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, *Oregon* stn 1981. 3 ♂ 3 ♀, USNM, NE of Punta Araguapiche, 457 m, 3 November 1957, *Oregon* stn 1982.

GUYANA—1 ♂, USNM, off Waini Beach, 137 m, 4 November 1957, *Oregon* stn 1993.

Description.—Body robust, integument thick, and entirely covered by densely set, short setae (Figure 29). Rostrum almost reaching or slightly overreaching distal end of antennular peduncle, nearly horizontal and straight in large adults, somewhat shorter, elevated, and broadly convex dorsally almost to tip in young; tip saber or spear shaped, 0.2-0.3 rostrum length, longest in adult. Rostral plus epigastric teeth 10-12 (mode 11; $N = 200$); teeth regularly closer from epigastric to ultimate; epigastric tooth located almost at level of dorsal extremity of cervical sulcus and fourth rostral tooth near level of orbital margin. Adrostral carina slender, extending from orbital margin almost to apex of rostrum; postrostral carina strong, long, almost reaching posterior margin of carapace; small tubercle present behind postrostral carina; antennal carina short but prominent. Orbital spine short, broad basally; postorbital spine slender, rather short, located posterodorsal to base of antennal spine; latter longest of lateral spines on carapace; branchiostegal spine moderately long; hepatic spine relatively short; pterygostomian spine lacking. Cervical sulcus sinuous, deep, ending lateral to postrostral carina at about midlength of carapace; cervical carina sharp. Hepatic sulcus almost horizontal posteriorly, merging with depressed area ventral to hepatic spine, from there inclining anteroventrally, and ending in pit below branchiostegal spine; hepatic carina accompanying anterior portion of sulcus sharp and prominent; branchiocardiac carina indistinct or barely perceptible; submarginal carina well marked, subparallel to free ventral margin of carapace.

Eye (Figure 30*E*) with basal article produced distomesially into pubescent, broad scale, bearing spinelike distal projection; ocular peduncle short, cornea broad, greatest diameter slightly more than twice that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace; prosartema ending slightly proximal to distal margin of first article; stylocerite extending only to about 0.45 of distance between its proximal extremity and mesial base of distolateral spine, produced distally into short, rather blunt spine; distolateral spine slender and moderately long, sensibly overreaching distal margin of article. Antennular flagella (Figure 30*A*) rather broad proximally, subfiliform distally, markedly unequal in length, but both long, and increasing proportionately in length with age: dorsal flagellum about 1.4 times carapace length and ventral about 1.2 times carapace length, in shrimp 8.5 mm cl, and 3.5 and 2 times carapace length, respectively, in shrimp 32 mm cl (flagella incomplete in all larger animals examined). Dorsal flagellum with distal half of proximal portion bearing longitudinal row of combs of long setae on slightly concave ventral surface (Figure 30*D*) and stiff short setae on remaining surfaces; stiff setae increasingly sparse toward tip of flagellum. Ventral flagellum exhibiting strong sexual dimorphism: in mature male, proximal portion resembling bottle brush, with mesial surface flattened and bearing longitudinal band of stiff, dense setae with apices directed proximally (Figure 30*B*); lateral surface armed with numerous, simple setae directed distally (Figure 30*C*); dorsal and ventral surfaces bearing flexible, plumose setae, most thickly set in comblike clusters. In females, ventral flagellum with proximal portion covered by long flexible setae.

Scaphocerite exceeding antennular peduncle by as much as 0.2 of its own length; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, as much as 5 times total length of shrimp. Mandibular palp (Figure 31*A*) relatively short, extending to about distal extremity of ischiocerite, proximal article 1.25 times as long as wide; distal article only slightly longer and narrower than proximal one, tapering to blunt tip. Maxillae and first and second maxillipeds as figured (Figure 31*B-E*). Two rudimentary arthrobranchiae on somite VII, near base of coxa of first maxilliped (Figure 31*Dg-g*^{1}), both anterior and posterior arthrobranchiae on somite VIII, and podobranchia on

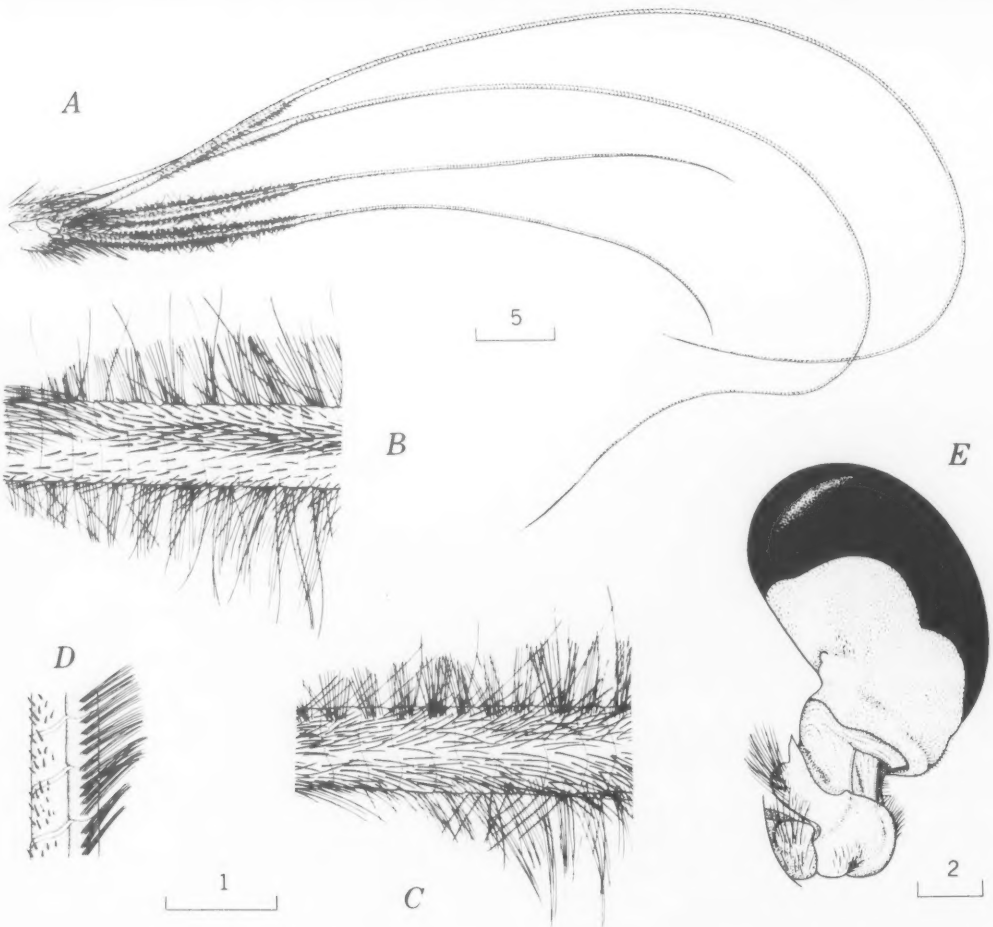

FIGURE 30.—*Pleoticus robustus*, ♂ 28 mm cl, south of Dry Tortugas, Fla. *A*, Antennular flagella. *B*, Mesial view of proximal part of ventral flagellum. *C*, Lateral view of same. *D*, Ventrolateral view of proximal portion (distal half) of dorsal flagellum. *E*, Eye, ♀ 34 mm cl, same locality.

corresponding second maxilliped; pleurobranchia, and anterior and posterior arthrobranchiae on somite IX (Figure 31*E*, *F*), pleurobranchiae present through somite XIV, and both arthrobranchiae through XIII. Third maxilliped exceeding antennular peduncle by at least 0.5 length of dactyl, or by dactyl and about 0.2 length of propodus.

First pereopod reaching between base and distal end of carpocerite. Second pereopod overreaching carpocerite by at least 0.5 length of dactyl, but by as much as entire propodus and 0.1 length of carpus. Third pereopod surpassing antennular peduncle by length of dactyl or by length of propodus and 0.2 that of carpus. Fourth pereopod extending to distal end of carpocerite or overreaching it by length of dactyl and 0.5 that of propodus. Fifth pereopod exceeding antennular peduncle by at least 0.5 length of dactyl or by length of dactyl and 0.4 that of propodus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First pereopod with moderately long, sharp spine at distomesial extremity of basis and ischium, and midlength of merus. In female, coxa of third pereopod expanded into thick, roughly trapezoidal plate,

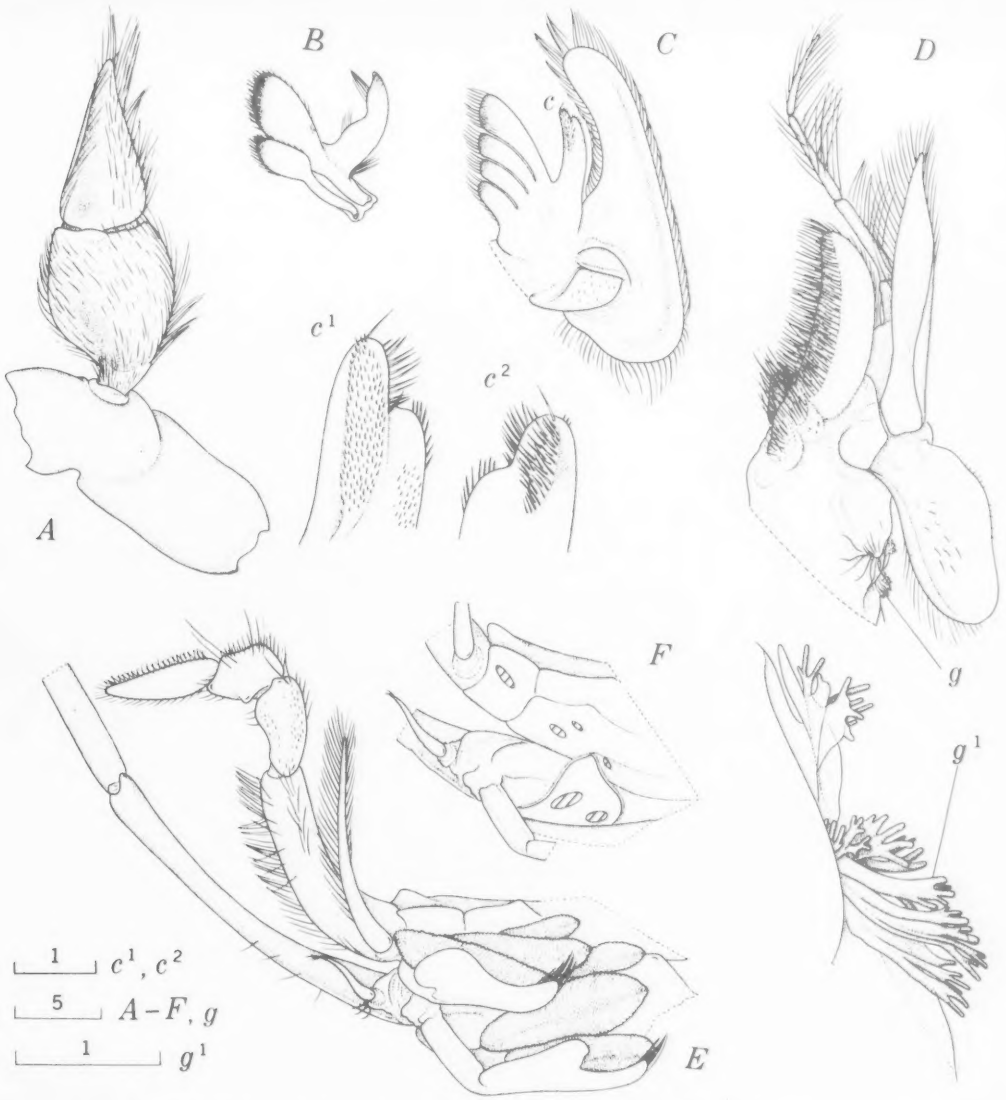

FIGURE 31.—*Pleoticus robustus*, ♀ 56 mm cl, off Dog Island, Lesser Antilles. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *c*, Endite of basipodite. c^1, Enlargement of *c*, ventral view. c^2, Dorsal view. *D*, First maxilliped. *g*, Rudimentary arthrobranchiae. g^1, Enlargement of *g*. *E*, Second maxilliped and proximal portion of third. *F*, Somites VIII and IX with proximal portions of second and third maxillipeds, showing attachments of gills.

raised in strong, densely setose prominence on ventral surface. Coxa of fifth pereopod in male bearing blunt spine on anteromesial margin; in female, coxa produced into setose, short plate.

Abdomen with middorsal carina from third through sixth somites, carina rounded on third, sharp and high from fourth posteriorly; sixth somite with small spine at posterior end of carina and paired, posteroventral spines. Telson with median sulcus rather shallow, short, occupying

about 0.35 length of telson, flanked by low carinae, latter becoming sharp posteriorly, reaching base of lateral spines; length of spine 1.1 to 1.5 times width of terminal portion at base; terminal portion length 3 to 4 times basal width. Mesial ramus of uropod overreaching apex of telson by about 0.2 of its length; lateral ramus, in turn, overreaching mesial by as much as 0.25 of its own length, and bearing minute, terminal, distolateral spine.

Petasma (Figure 32*A, B*) cincinnulate along entire median line, with distal margin spinulous; midrib of dorsolateral lobule broadest proximally, and ending distally in narrow, sometimes sinuous tip; ventrolateral lobule almost entirely sclerotized, but produced distally into rather flexible, elongate flap, strongly inclined toward median lobe; ventral costa with free terminal part curved dorsally and armed with minute spines on distal margin.

Appendix masculina (Figure 32*C, D*) elongate, deeply excavate ventromesially for reception of appendix interna, broad proximal part raised in longitudinal, lateral rib extending to base of narrower distal part; strong dorsal thickness along distal part curving around terminal margin, there bearing tuft of rigid setae. Appendix interna considerably shorter than appendix masculina and consisting of short bulbous basal portion and elongate, narrow but thick distal portion. Ventrolateral spur abruptly narrowing slightly distal to midlength, becoming fingerlike.

Thelycum (Figure 33*A*) microscopically setose-punctate (Figure 33*B*), with paired subtriangular projections on anteriormost part of sternite XIV, usually inclined anteriorly, overlapping posterior margin of sternite XIII; posterior part of sternite XIV strongly bulging, often bearing midlongitudinal groove. Median plate of sternite XIII delimited anteriorly by paired deep depressions, and armed with strong anteromedian rib; sternite XII with central elevation, and paired, transverse marginal ridges overlapping sternite XIII.

Color.–Both coloration, as previously indicated by various authors, and color pattern are very variable. Burkenroad (1936) described fresh, though dead, juveniles, caught in the waters off Alabama, as follows: "Eyes deep reddish-brown with greenish reflections; gastric gland grayish-brown with light yellow-green flecks, stomach red; body pale orange-red, with a band of deeper salmon on the posterior part of each pleonic tergum; an iridescent blue-green area on the dorsum of each pleonic segment and of the telson." Springer (1951b) indicated that shrimp taken in the northern Gulf of Mexico were "brick red as they come from the water." Anderson and Bullis

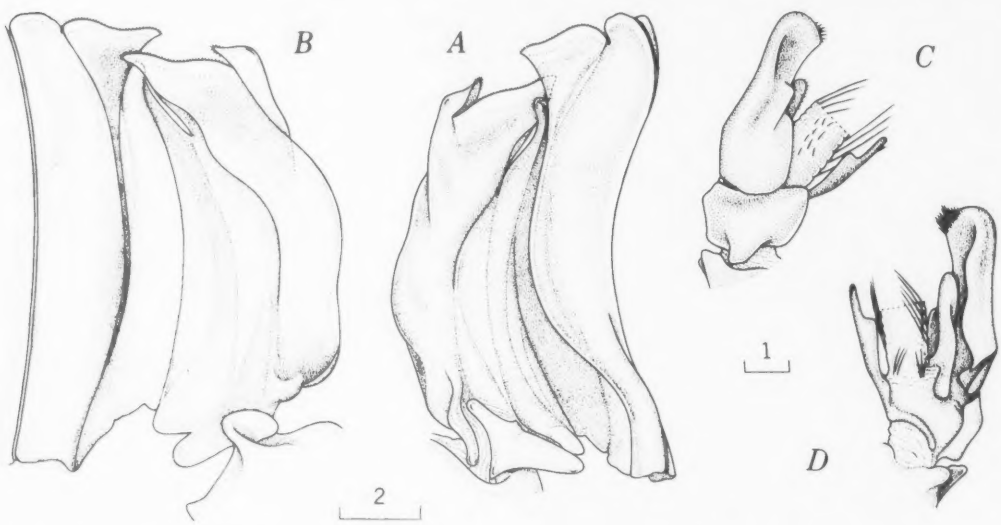

FIGURE 32.—*Pleoticus robustus*, ♂ 32 mm cl, east of Península Valiente, Panama. *A*, Petasma, dorsolateral view of left half. *B*, Ventrolateral view (extended). *C*, Right appendices masculina and interna, lateral view. *D*, Mesial view.

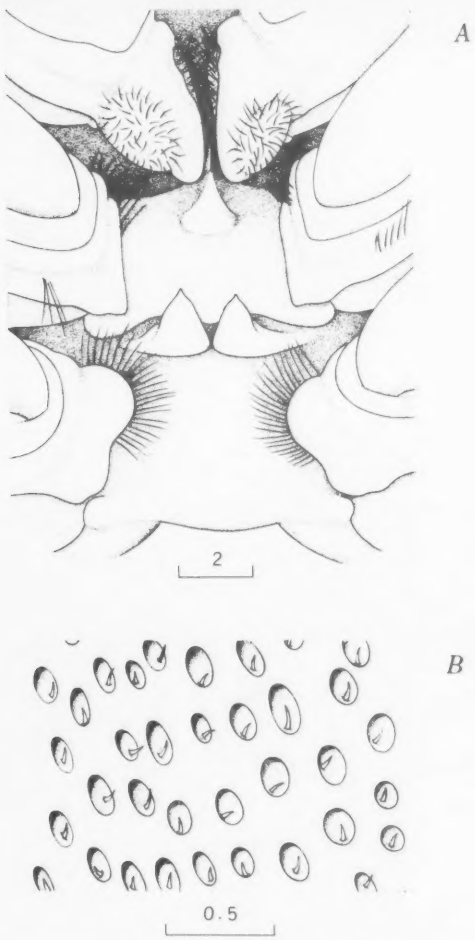

FIGURE 33.—*Pleoticus robustus*, syntype ♀ 49 mm cl, south of Curaçao. *A*, Thelycum, ventral view. *B*, ♀ 61 mm cl, west of Ríohacha, Colombia. Portion of sternite XIV showing seta-bearing depressions.

(1970) found that in animals observed from a submarine the "Color varied from grayish pink to red—similar to color observed on trawl-caught specimens." A diel color change was pointed out by Bullis (1956), who stated "nighttime catches are typically bright red, while catches landed during daylight hours are a light pink." Recently, García del Barco (1972) has confirmed this circadian variation.

My examination of large quantities of freshly collected animals during a 1969 cruise of the *Oregon II* in the Caribbean (Puerto Rico to Antigua) corroborated earlier observations of the great variation in this character, and disclosed the existence of many color patterns. The overall body color ranges from off white through pink and salmon to deep red, and the color pattern may consist of a few bright lines—mostly on various carinae—or even an abundance of strong markings. Opaque white and, particularly, reddish with white markings individuals were very common, whereas salmon ones, apparently similar in color to those shrimps from the northern Gulf of Mexico described by Burkenroad, were infrequent.

Descriptions of three color phases observed follow:

Pink-red phase: Body pink, marked with red and white. Gastric region intense pink; rostrum brilliant red with tip paler; anterior rostral teeth with bases red and apices light, but teeth posterior to orbital margin with brilliant deep red apices; small white patch in area between orbital, postorbital, and antennal spines; cardiac region light red; anteroventral border as well as antennal and cervical carinae and contiguous spines deep red; longitudinal opaque white stripe tapering from anteroventral margin (dorsal to branchiostegal spine) to depressed area below hepatic spine, from there broadening abruptly along entire cervical sulcus, then tapering again to about level of third pereopod, there forming narrow, short stripe, continuing along posterior margin of carapace then recurving anteriorly, parallel to ventral margin, to level of base of second maxilliped, ending there in elongate white patch; deep red stripe inserted between arms of pink one. Abdomen light pink anteriorly, increasingly deep pink posteriorly, turning red on sixth somite; first five somites with posterior margin of tergum bordered by transverse red band, and posterior margin of pleuron with white band continuing anteriorly onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite brilliant red. Telson light red, with carinae, lateral margins, and transverse band proximal to terminal portion deep red. Basal podomere of uropod pink with lateral margin red; lateral ramus intense pink except for deep red tip; mesial ramus with pink proximal portion followed by white transverse band and latter, in turn, by red marking covering distal portion except for white mesial patch. Antennular peduncle light red, but apex of stylocerite and distolateral

spine brilliant red, and prosartema pink; flagella red proximally fading to pink distally. Antenna pink. Third maxilliped and pereopods with coxa and basis white, remaining podomeres reddish. Pleopods with basis white but bearing pink semicircular, lateral patch; exopods white proximally, with red and pink transverse bands on midportion, and white distal patch; endopods white with pink band at midlength. Eye with peduncle white, and separated from cornea by two lines, proximal pink and distal red; basal article pink.

Salmon phase: Carapace anterior to cervical sulcus deep salmon, cardiac region, and ground color of abdomen pale salmon; rostrum (except for white tip) and branchiostegite bright reddish orange, that on branchiostegite sharply delimited dorsally along hepatic sulcus and branchiocardiac carina; apices of rostral teeth and spines, as well as postrostral and cervical carinae deep orange-red; bases of teeth and spines, and cervical sulcus opaque white. Tergum of first through fifth abdominal somites with posterior, transverse band of reddish orange, band broad on middorsal portion, tapering ventrally to base of pleuron, from there extending along posterior margin and onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite deep reddish orange. Telson with ground color deep salmon, except for yellowish white basal portion; lateral portion of margins and paired carinae bright orange-red, giving rise on each side to angle with vertex on spine. Pereopods with coxa and basis white, and remaining podomeres salmon with longitudinal orange-red strip. Pleopods yellowish, but basis with roughly semicircular lateral white patch subtended by bright reddish orange stripe on lateral margin. Uropod mostly salmon; lateral ramus with distalmost portion bright red and mesial ramus with tip white.

Opaque white phase: Ground color opaque white with very pale salmon suffusion, more intense on rostrum; however, tip of rostrum, teeth and adrostral carina corneous; cardiac region grayish white, and entire branchiostegite milky white; branchiostegal and hepatic spines as well as cervical and postrostral carinae orange-red; longitudinal streak of orange-red extending posteriorly from dorsal end of cervical carina well beyond midlength of carapace. Pleura of first five abdominal somites with milky white U-shaped band following contour of margin; middorsal carina and posterior and ventrolateral margins of sixth somite orange-red. Telson almost white with median sulcus orange-red. Lateral ramus of uropod with oblique, milky white stripe at base of distal fourth, and subtended distally by intense salmon colored band and this, in turn, by white tip; mesial ramus with large, proximomesial, suboval, milky white patch bounded laterally by salmon band, and with distalmost portion milky white. Antennular peduncle deep salmon proximally, becoming pink distally; prosartema, antennular flagella, and antenna pink. Third maxilliped and pereopods with coxa and basis white, and remaining podomeres white with very light pink suffusion. Pleopods pinkish white bearing milky white, semicircular, lateral patch. Ocular peduncle white, and bearing orange-red stripe along border with cornea.

Maximum size.–The largest male examined by me has a carapace length of 42 mm, about 173 mm tl, and the largest female, 61.5 mm cl, about 219 mm tl; however, Klima (1969), in his work on length-weight relation, recorded larger specimens of both sexes, a male within the range of 180-184 mm tl and a female within 225-229 mm tl.

The sizes at which maturation occurs were determined by Anderson and Lindner (1971) to be at about 125 mm tl in males and about 155 mm tl in females.

Geographic and bathymetric ranges.–Pleoticus robustus ranges (Figure 34) from immediately south of Martha's Vineyard, Mass. (40°00′15″N, 70°54′00″W), through the Gulf of Mexico, and the Caribbean to French Guiana (07°05′N, 52°47′W), occurring on the upper continental slope at depths between about 180 and 730 m (Figure 9). It has been found only occasionally north of Cape Hatteras, and seems to be scarce off the Guianas. Inasmuch as this species has not been reported from Brazilian waters, French Guiana is cited here as the southernmost limit of the species on the basis of samples taken during the *Oregon* cruises off northeastern South America. The southern range of the species given by Bullis and Cummins (1963) was based on the same collections; consequently their statement that the royal red reaches Brazil should be understood to mean that it extends to about the border between French Guiana and Brazil.

The highest concentrations of *P. robustus*—off the northeast coast of Florida and in the north-

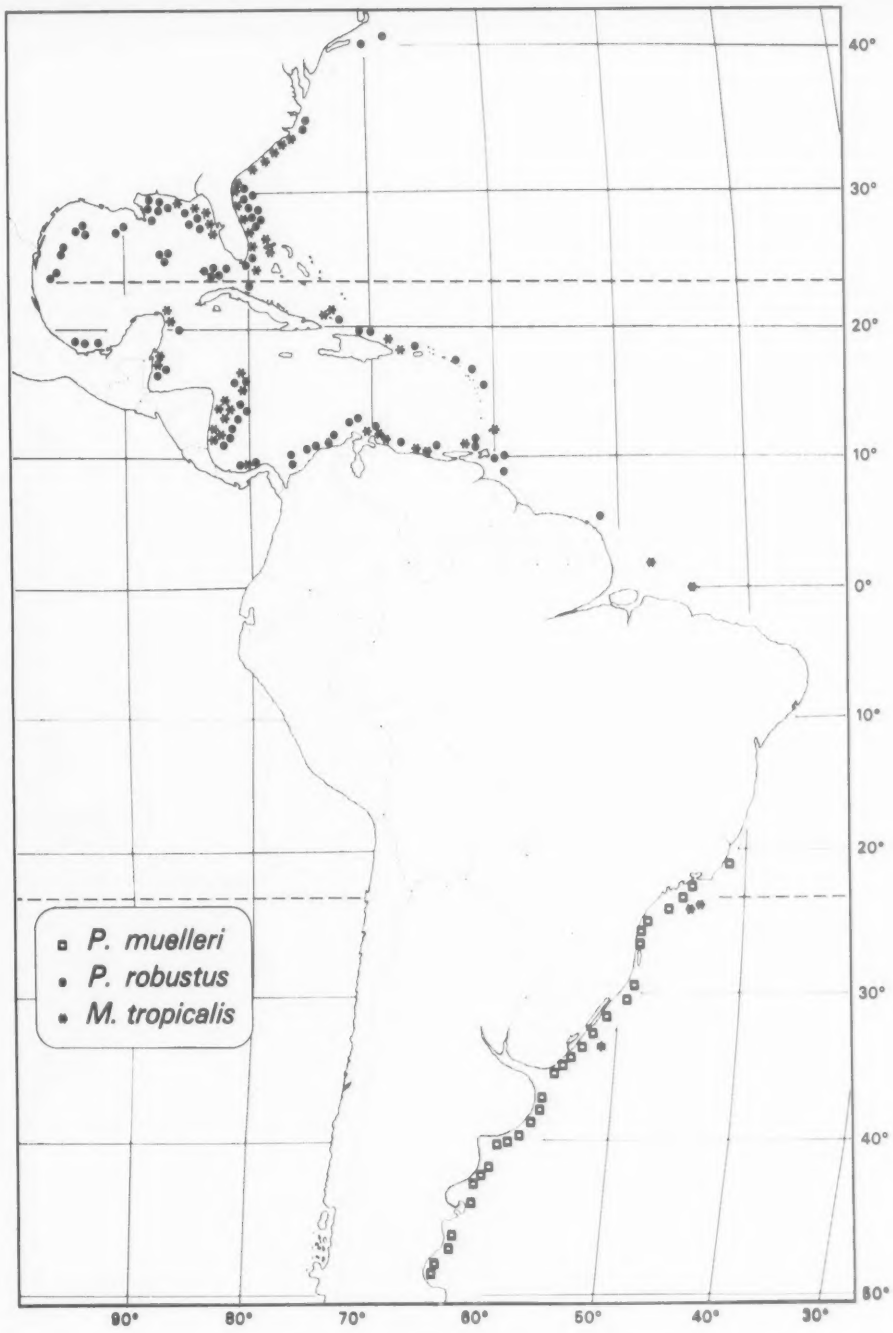

FIGURE 34.—Ranges of *Pleoticus muelleri*, *Pleoticus robustus*, and *Mesopenaeus tropicalis* based on published records and specimens personally examined.

eastern part of the Gulf of Mexico—occur at depths between 250 and 475 m. The species is scarce in less than 256 m, and not abundant at depths greater than 500 m. If the data are correct, the male found in 137 m off Guyana at *Oregon* stn 1993 represents an extremely rare occurrence of the shrimp in waters shallower than 180 m, as does the presence of the species at 70 m (at *Oregon* stn 2669, 18°31′N, 66°47.5′W, north of Puerto Rico), reported by Bullis and Thompson (1965). Although Roberts and Pequegnat (1970) stated that this shrimp has been found at depths as great as 500 fm (915 m), there is no precise record of its presence below 400 fm (732 m). Their statement seems to have been based on a catch from the *Alaminos,* in 289-472 fm (529-863 m); however, their remaining records, as well as those of all others, suggest that the specimens obtained in that haul were caught in the shallower part of the depth range cited.

Throughout the Caribbean and northeastern South America, the royal red shrimp seems to be rather sparsely distributed; various explorations by the *Oregon* and *Oregon II* in the region have indicated a dense concentration only off Cabo de la Vela, Colombia.

Affinities.–Pleoticus robustus can be separated from *P. muelleri,* the only other western Atlantic representative of the genus, by the following characteristics: the densely pubescent body, the relatively short prosartema, which does not overreach the distal margin of the first antennular article, the presence of a branchiostegal spine, the lack of an orbital spine, and the disposition of the submarginal carina which is subparallel to the free border of the carapace along its entire length. The external genitalia of the two species are also quite different: whereas in the petasma of *P. robustus* the row of cincinnuli occupies the entire median line, the ventromedian lobule is flexible and entire distally, and the ventral costa is plain, in *P. muelleri* the row of cincinnuli extends only along the proximal 0.4 of the median line, the ventromedian lobule is produced distally in cornified oval and hooklike projections, and the distal part of the ventral costa bears a flange along the inner border. Also, the thelycum of *P. robustus* exhibits a pair of anterior triangular projections on the flexible anterior part of sternite XIV, and a median ridge on sternite XIII, whereas that of *P. muelleri* bears nothing more than a pair of minute tubercles on the heavily sclerotized anterior part of sternite XIV, and a strong median projection on sternite XIII.

Spermatophore.–Compound spermatophore (as attached to female) consisting of broad, dorsoventrally depressed geminate body, with conspicuous transverse fold at about midlength, and bearing anterolateral wings; also provided with sculptured lateral flaps, and produced posterolaterally in short flanges (Figure 35).

Ventral and lateral walls of each spermatophore (Figure 36*A*) thick, opaque, fusing imperceptibly, their anterior margins broad and perpendicular to medial line. Spermatophore lacking anterior lobe, deeply concave at base of wing, there bearing conspicuous constriction; transverse angular fold present at about midlength, followed by depressed caudal half. Dorsomesial wall (Figure 36*C*) largely translucent, with globular anterior evagination (Figure 36*B*) markedly expanding lumen of sperm sac; posterior part of latter attenuated caudally by close proximity of opposing walls. Flap broad anteriorly and merg-

FIGURE 35.—*Pleoticus robustus,* compound spermatophore attached to female, ♀ 44 mm cl, west of Quita Sueño Bank, western Caribbean (setae omitted).

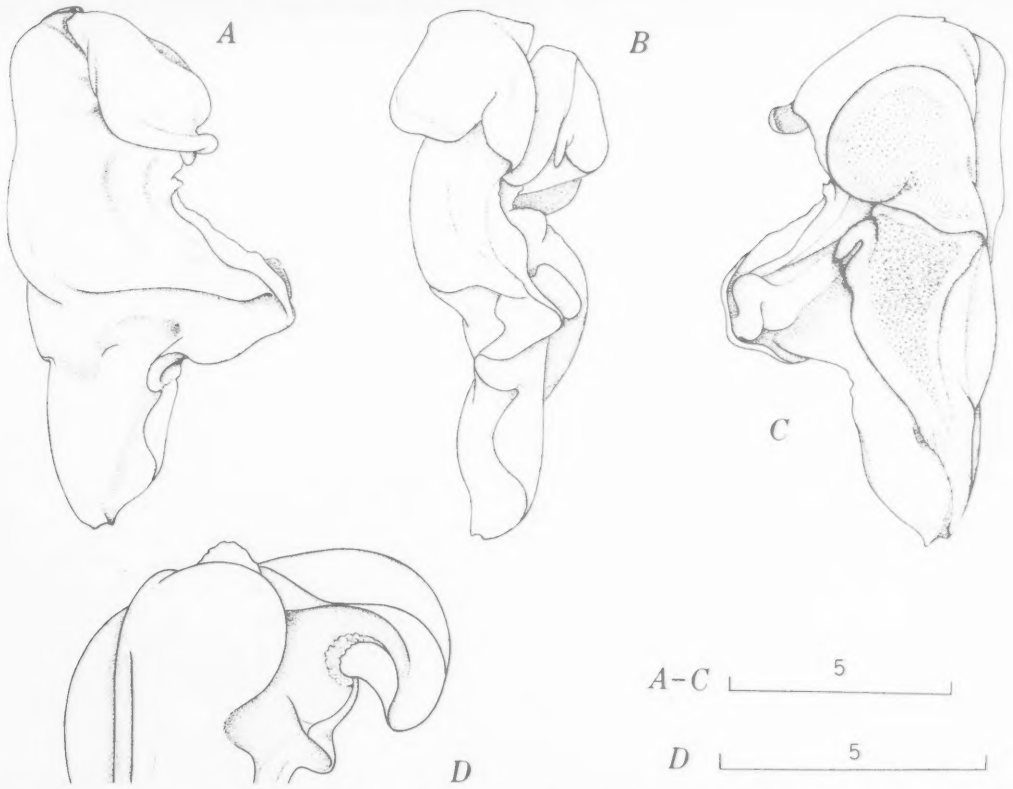

FIGURE 36.—*Pleoticus robustus*, ♂ 37 mm cl, east of St Lucie Inlet, Fla. *A*, Left spermatophore dissected from terminal ampulla, ventrolateral view. *B*, Lateral view. *C*, Dorsal view. *D*, ♂ 38 mm cl, off St Augustine, Fla. Distal portion of left spermatophore (wing extended).

ing insensibly with lateral base of flange. Wing (Figure 36*D*) heavy, opaque, with broad base forming rounded lobe continuous with lateral wall, and tapering to short, blunt tip. Flange short, broadly subelliptical. Dorsal plate nearly triangular, anteriorly fitting snugly into deep groove of dorsomesial wall.

Compound spermatophore applied to female with anterior margin lying approximately at posterior margin of gonophores, and sperm masses—protruding through dorsomesial walls (apparently torn by forced release of those masses during mating)—lodged in paired concavities of sternite XIII. Bases of the wings attached to sternite XIII, their distal parts resting on same sternite, and on ventral articular membranes of fourth pereopods. Lateral flaps affixed to sternite XIV, and just posterior to transverse folds of sacs, geminate body sloping caudodorsally over bulge of sternite XIV; adjoining flanges resting on posterior thoracic ridge. Wings and lateral flaps lie under (dorsal) setose coxae of fourth and fifth pereopods, respectively, which also aid in securing compound spermatophore on female. Dorsal plates, subjacent (dorsally) to caudal part of sacs, directly anchored to sternite XIV, thus helping to hold spermatophore in place.

The exceedingly large spermatophores of this shrimp appear to become attached to the female more firmly than those of many other penaeids with open type thelyca. This statement is based on the observation that females with attached spermatophores are frequently found in collections, whereas in other species with open type thelycum such females are rarely encountered. Most of the compound spermatophores that I have

detached from impregnated females are practically empty. This suggests that the sperm are released with the entire spermatophore present, i.e., that the spermatophore is not torn or split leaving the sperm masses with the paired wings flanking them on the female while the geminate body and adjoining flanges fall away, as seems to occur in some members of the subgenus *Litopenaeus*, genus *Penaeus*.

Reproduction.–Anderson and Lindner (1971) reported that on the St. Augustine Grounds, *P. robustus* probably spawns throughout the year, with a peak between January and May. Recruitment begins when the shrimp are approaching 1 yr of age and are less than 100 mm tl; maturity is reached in about 3 yr. Most shrimp on the grounds are mature, and the life span appears to be no less than 5 yr.

The larvae of *P. robustus* are unknown. Burkenroad (1936) identified as "juveniles" the only postlarvae of the species ever recorded, specimens that I have examined. Curiously, Anderson and Lindner (1971) found neither larval nor postlarval stages in a large number of plankton samples collected over an extensive area seaward of the St. Augustine Grounds. They stated that only a single larva was considered as possibly belonging to *"Hymenopenaeus."*

Ecological notes.–In the northestern Gulf of Mexico and off the southeastern coast of the United States, this shrimp has been found within a temperature range of 5°-15°C, and is commercially abundant betwen 9° and 12°C (Bullis 1956; Bullis and Cummins 1963). The preference of *P. robustus* for this range of temperature was revealed by the observations of Bullis and Cummins, who stated that within 1 or 2 days after two incursions of cold bottom water off the northeast coast of Florida, shrimp moved inshore to waters 75 m shallower than those where they had been observed previously. Later, Roe (1969) reported that the maximum densities of this shrimp is in water temperatures of 9° to 10°C.

Commercial concentrations of royal red have been reported (Bullis 1956; Bullis and Rathjen 1959; Roe 1969) to occur on the following types of bottoms: blue-black terrigenous silt and silty sand off the Mississippi River Delta; whitish, gritty, calcareous mud off Tortugas; and basically similar sand or silty sand (called "green mud" by the fishermen) off the northeast coast of Florida.

Anderson and Bullis (1970) presented direct observations of this shrimp made from the submarine *Aluminaut* off Daytona Beach, Fla., at a depth of 459 m. They stated that "The bottom was remarkably free from obstructions and consisted of a grayish, loosely constituted sediment that readily clouded the water at the least disturbance. It was formed into a myriad of shallow depressions and mounds, pitted with holes. . . . Bottom photographs had previously indicated that royal-red shrimp stayed on the sea-floor surface, but we saw numerous shallow furrows (1 to 3 feet long) in the bottom in which royal-red shrimp were partly buried. They apparently do not burrow as deeply or completely as do brown and pink shrimp. We believe the shrimp plow into the bottom in search of food rather than protection, and that this feeding activity produces the grooves or furrows."

Remarks.–Smith (1885) cited 14 males and 4 females in USNM lots 6907 and 6908. My examination of this material has shown that the first lot consists of 2 males and 7 females, but the second lot includes 2 males and 5 females of *"Hymenopenaeus" robustus* and 1 female of *Penaeopsis serrata* (Bate 1881). Consequently Smith's statement is in error since there are only 4 males and, furthermore, the total number of females (including that of the latter species) must have been either 13 or 12 if one of them is missing from the lots. In the original description of the species, Smith stated that the proximal portion of the ventral antennular flagellum "is densely hairy in the male"; however, the marked difference that occurs between the pubescence of the flagellum in the male and the female has not been cited in subsequent morphological studies of the shrimp. Here, for the first time, detailed accounts of the setation of the ventral flagellum in both sexes are presented.

The petasma of *P. robustus* has been described previously by various investigators. Smith (1885) gave the first brief account. Later, A. Milne Edwards and Bouvier (1909) described and illustrated it in more detail; however, the two figures presented by them include several inaccuracies which were pointed out by Burkenroad (1936). In the same publication, the latter gave an accurate description of this structure. More recently, Roberts and Pequegnat (1970) presented observations as well as a sketch of the petasma, and Anderson and Lindner (1971) have provided the

most complete illustration available. The account of the petasma herein, utilizing Kubo's (1949) terminology, is given in order that comparisons of this species with others treated in this work may readily be made.

Economic importance.–Pleoticus robustus is the only deep-water penaeoid in the western Atlantic that is now commercially exploited.

This large wide ranging shrimp has been found in commercial quantities only in three areas off the coast of the United States:

1. off northeast Florida on the St. Augustine Grounds
2. south to southwest of Dry Tortugas Islands
3. southeast of the Mississippi River Delta to off Tampa Bay.

The commercial potential of the species was reported by Springer (1951b) and Springer and Bullis (1952) on the basis of its abundance off the Mississippi Delta. Subsequent explorations in the northern and northeastern Gulf of Mexico confirmed previous findings, and disclosed the concentration off the Dry Tortugas (Springer and Bullis 1954; Bullis 1956). Later, Bullis and Rathjen (1959) investigated the density of the populations off the southeast Atlantic coast of the United States and indicated the high potential of the St. Augustine Grounds, the exploitation of which began in 1962 (Cummins and Rivers 1962). The grounds in the northeastern Gulf of Mexico remained unexploited until this decade, when fishing was initiated. Total landings of royal red shrimp in 1976 (Anonymous 1977) amounted to 167,000 pounds (75,751 kg), heads-off, caught almost entirely off northwest Florida.

Pleoticus muelleri (Bate 1888)

Figures 9, 34, 37-42

Philonicus mülleri Bate 1888:275, pl. 39, fig. 1-2 [syntypes: 5 ♂ 25 ♀, BMNH, off Montevideo, Uruguay, 35°02'S, 55°15'W, 13 fm (24 m), 25 February 1876, *Challenger* stn 321]. Fowler 1912:543.

Pleoticus mülleri. Bate 1888:939. Berg 1898:38. Fesquet 1933:6, fig. 1-4, pl. 1-8; 1936:61. Barattini and Ureta 1960:49.

Pararteмesia carinata Bouvier 1905b:748 [syntypes: 1 ♂ 3 ♀, MP 59, off mouth Río de la Plata, 35°42'S, 56°20'W, 44 fm (80 m), *Hassler*. 1 ♀, Río de la Plata, Montevideo, 7 fm (13 m), *Hassler*].

Haliporus carinatus. Bouvier 1906b:4.

Haliporus mülleri. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:214, fig. 38-44, pl. 2, fig. 9-10. Pesta 1915:102.

Hymenopenaeus mülleri. Burkenroad 1936:103. Fesquet 1941:64. Rioja 1941:200, fig. 13, 17; 1942:659, fig. 20, 21, 30, 31. Anderson and Lindner 1945:288. López 1954:46. Popovici and Angelescu 1954:505. Lindner 1957:4. Angelescu and Boschi 1960:1, fig. 4, 10-16, pl. 1, 2, 5, 6. Eldred and Hutton 1960:91. Boschi and Angelescu 1962:1, fig. 1-17, pl. 1, 2. Boschi 1963:5, fig. 4. Mistakidis and Neiva 1964:471. da Silva 1965:4. Tremel and Mistakidis 1965:2. Mistakidis 1965:1. Neiva and Mistakidis 1966:4, fig. 4a, b. Mistakidis and Neiva 1966:434. Idyll 1969:642. Pérez Farfante 1970:13, fig. 3I-K. Iwai 1973:44.

Hymenopendeus mülleri. Carcelles 1947:4, pl. 1, fig. 2.

Hymenopenaeus muelleri. Boschi 1964:38. Holthuis and Rosa 1965:1. Boschi 1966:452. Boschi and Mistakidis 1966:1. Boschi and Scelzo 1969a:3; 1969b:152, pl. 1. Boschi 1970:65; 1974:3. Scelzo and Boschi 1975:193. Boschi and Scelzo 1976:1. Boschi 1976:63.

Camarão barbado. Tremel et al. 1964:8.

Vernacular names: langostino, langostín (Uruguay, Argentina), camarão de Santana, lagostinho da Argentina, camarão vermelho, camarão barbado, camarão ferro (Brazil).

Material

BRAZIL—Espírito Santo: 2 ♀, USNM, off Praia de Santana, June 1962, G. de Souza Neiva. Rio de Janeiro: 2 ♀, USNM, off Macaé, 23 m. Superintendência do Desenvolvimento da Pesca, Seçao de Pesquisas. 9 ♀, USNM, Ilha dos Franceses, Cabo Frio, 50 m, 17 October 1975, Staff Instituto de Pesquisas da Marinha, Estaçao de Biologia Marinha. 4 ♀, YPM, off Rio de Janeiro, May 1934, M. W. Feingold. 1 ♀, USNM, off Ilha Grande, 23 m, 8 December 1961, *Calypso* stn 115. 3 ♀, USNM, off Baía da Ilha Grande, 36 m, 9 December 1961, *Calypso* stn 122. São Paulo: 3 ♂, USNM, Ubatuba, 15 m, 10 April 1972, J. de Abreu. 1 ♂ 5 ♀, MP, S of Ilha de São Sebastiaõ, 25 m, 11 December 1961, *Calypso* stn 135. 15 ♂ 9 ♀, USNM, Baía de Santos, 6 September 1964, G. Vazzoler. 4 ♂ 3 ♀, USNM, Baía de Santos, 29 September 1964, G. Vazzoler. 3 ♂ 3 ♀, USNM, Baía de Santos, 1 October 1962, G. de Souza Neiva. 3 ♂ 5 ♀, USNM, Farol de Moela, Santos, 9 September 1964, G. Vazzoler. Paraná: 1 ♀, USNM, off Paranaguá, Ex. H. Jakobi. Santa Catarina: 37 ♂ 47 ♀, MP, off Ensenada de Tijucas, 18 m, 16 December 1961, *Calypso* stn 149. 5 ♀, USNM, Armação de Piedade, 19 November 1965,

E. Tremel. Rio Grande do Sul: 16 ♂ 14 ♀, MP-USNM, off Barra Casino, 21 m, 18 December 1961, *Calypso* stn 153. 1 ♂ 1 ♀, USNM, Xuí, 19 m, 8 January 1962, *Calypso* stn 183.

URUGUAY—8 ♂ 9 ♀, MP-USNM, off Punta del Palmar, Rocha, 20-22 m, 21 December 1961, *Calypso* stn 156. 26 ♂ 35 ♀, MP, off Punta del Este, 57 m, 21 December 1961, *Calypso* stn 157. 1 ♂, MP, N of La Paloma, 33 m, 21 December 1961, *Calypso* stn 158. 34 ♂ 63 ♀, MP-USNM, N of Cabo Santa María, 25 m, 8 January 1962, *Calypso* stn 182. 26 ♂ 48 ♀, MP-USNM, off Laguna Rocha, 30 m, 22 December 1961, *Calypso* stn 161. 7 ♂ 7 ♀, MP, off Punta Negra, 18 m, 27 December 1961, *Calypso* stn 167. 1 ♂ 3 ♀, MP, off Maldonado, 115 m, 21 December 1961, *Calypso* stn 160. 1 ♂ 5 ♀, ANSP, Bahía Maldonado, W. H. Rush. 8 ♂ 15 ♀ syntypes of *Philonicus mülleri*, BMNH, off Montevideo, 13 fm (24 m), 25 February 1876, *Challenger* stn 321.

ARGENTINA—1 ♂ 3 ♀ syntypes of *Parartemesia carinata* Bouvier, MP 49, mouth of Río de la Plata, 44 fm (80 m), *Hassler*. 13 ♂ 11 ♀, YPM, "Buenos Aires," 15 June 1936. 2 ♀, USNM, Mar del Plata, 15 December 1922, H. M. Smith. 2 ♂ 2 ♀, UMML, Mar del Plata, January 1959 Ex. E. Boschi. 2 ♀, Quequén, 7 January 1924, G. Haedo. 1 ♀, USNM, Puerto Madryn, Chubut, Ex. Museo Argentino de Ciencias Naturales. 1 ♂ 2 ♀, Rawson, Chubut, November 1963, E. Boschi.

Description.–Body robust, integument thick, polished except for dorsally pubescent rostrum, narrow bands of setae flanking middorsal carina of sixth abdominal somite, and similar bands along borders of median and lateral sulci of telson; also broad bands of longer setae flanking paired longitudinal ridges of mesial ramus of uropod. Rostrum horizontal (Figure 37), straight, rather short, not reaching beyond distal 0.3 length of second antennular article, with dorsal margin slightly convex, and ventral margin almost straight, occasionally with apical concavity. Rostral plus epigastric teeth 7-13 (mode 9; $N = 200$), epigastric tooth separated from first rostral by interval similar to that between first and second, epigastric tooth located at level of dorsal extremity of cervical sulcus and usually fourth tooth at level of orbital margin. Adrostral carina slender, extending from orbital margin to base of ultimate tooth; postrostral carina strong, long, almost reaching posterior margin of carapace, where flanked by paired depressions. Orbital spine short; broad postorbital, antennal, and hepatic spines moderately long and sharp; pterygostomian and branchiostegal spines lacking. Cervical sulcus only slightly sinuous, deep, with dorsal extremity situated relatively far from postrostral carina; cervical carina sharp. Hepatic sulcus nearly horizontal from posterior end to depression below hepatic spine, there turning anteroventrally and reaching to pterygostomian region; hepatic carina accompanying anterior part of sulcus sharp; branchiocardiac carina lacking; submarginal carina well marked, horizontal posteriorly, turning anteroventrally at about midlength of carapace and then continuing close to free ventral margin of carapace almost to pterygostomian region.

Eye (Figure 38) with basal article produced distomesially into pubescent, broad scale; ocular peduncle short; cornea broad, greatest diameter slightly less than 2 times that of base of ocular peduncle, its proximal margin moderately slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace; prosartema long, reaching distal 0.4 of second antennular article; stylocerite spiculiform distally, moderately long, its length about 0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter sharp and long. Dorsal flagellum filiform, ventral flagellum broad proximally, tapering distally, and bearing marginal (lateral and mesial) patches of long setae proximally, latter continuous with single row distally; in shrimp 24 mm cl, ratio of length of

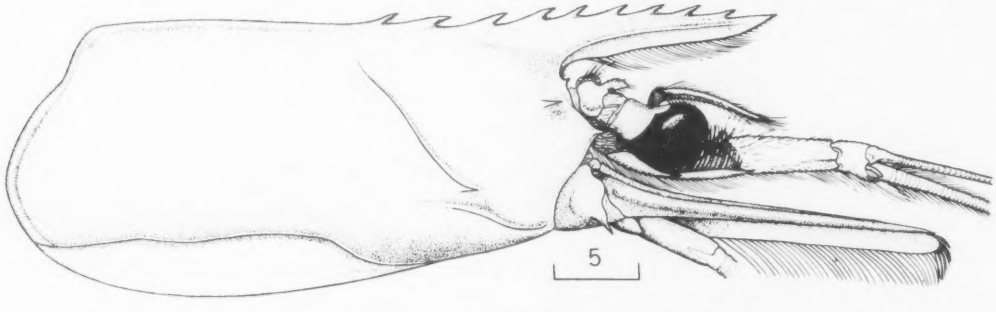

FIGURE 37.—*Pleoticus muelleri*, ♀ 27.5 mm cl, off Laguna Rocha, Uruguay. Cephalothorax, lateral view.

FIGURE 38.—*Pleoticus muelleri*, ♀ 33 mm cl, north of Cabo Santa María, Uruguay. Eye.

dorsal and ventral flagella to that of carapace 2.90 and 2.25 respectively and in shrimp 30 mm cl, 2.5 and 2.0. Scaphocerite exceeding antennular peduncle by 0.2 to 0.3 its own length; lateral rib ending in long spine falling short of distal margin of lamella; antennal flagellum almost 3 times total length of shrimp. Third maxilliped reaching almost to distal margin of third antennular article or surpassing it by as much as 0.5 length of dactyl.

First pereopod reaching between proximal 0.3 and distal margin of carpocerite. Second pereopod overreaching antennular peduncle by almost length of dactyl or by entire propodus. Third pereopod surpassing antennular peduncle by at least length of dactyl and, at most, by propodus and 0.15 length of carpus. Fourth pereopod exceeding carpocerite by as much as entire length of dactyl. Fifth pereopod, longest of all appendages, exceeding antennular peduncle by length of dactyl and 0.15 or 0.20 length of propodus. Order of pereopods in terms of their maximal anterior extensions: first, fourth, second, third, and fifth. First pereopod with spine at midlength of mesial border of basis very long and sharp, and spine on ischium sharp, but smaller than that on basis; second pereopod with setose, squamiform tubercle on distoventral border of coxa, and with long sharp spine on basis. In females, coxa of fifth pereopod produced as rounded, posteromesially directed plate, terminating in tooth anteriorly, plate hinging on horn of posterior plate of sternite XIV; coxa of fourth pereopod narrow, thick, with two rounded mesial projections, base of posterior one hinging on anterior horn of median plate of sternite XIII; coxa of third pereopod produced mesially in subtrapezoidal plate provided with long mesial setae overlapping those of opposite plate, coxa bearing gonopore on dorsomesial surface. In males, coxa of fifth pereopod with large tooth on anterior margin.

Abdomen with middorsal carina along entire length, carina low and rounded from first to third somites (imperceptible in young), and keellike posteriorly; posterodorsal margins of third through fifth somites with median incision; sixth bearing small, sharp spine at posterior end of carina, and small posteroventral spines. Telson with median sulcus moderately deep anteriorly, posteriorly bearing median elevation merging into convex terminal portion; lateral spines moderately long; length of terminal portion about 4 times width at base. Mesial ramus of uropod surpassing apex of telson by 0.15-0.25 of its own length; lateral ramus slightly overreaching mesial ramus and bearing small, terminal distolateral spine.

Petasma (Figure 39*A*, *B*) cincinnulate along proximal 0.4 of median line; distal part of ventromedian lobule cornified, forming plate bearing terminal suboval projection and lateral spurlike projection; much of lateral lobe heavily sclerotized, overlapping ventral costa, and with shallow lateral emargination marking base of distal portion; latter flexible, subelliptical, directed toward, and partly covered (dorsally) by, ventromedian lobule; ventral costa bearing membranous flap, broadening distally and terminating in paired unequal convexities; free terminal part of costa forming dorsally directed, strongly curved, sharp projection.

Appendix masculina (Figure 39*C*, *D*) elongate, with heavily sclerotized dorsolateral portion and flexible, subelliptical mesial portion. Appendix interna spatulate, embracing ventromesial margin of appendix masculina proximally, and bearing distolateral tuft of rigid, long setae. Basal sclerite with deep distolateral groove along base of sharp dorsal ridge; ventrolateral spur relatively short.

Thelycum (Figure 40) microscopically setosepunctate, with posterior plate on sternite XIV often divided by median longitudinal groove, and bearing lateral elevations terminating anteriorly in small knob; short anterior part of sternite XIV heavily sclerotized, forming slightly convex,

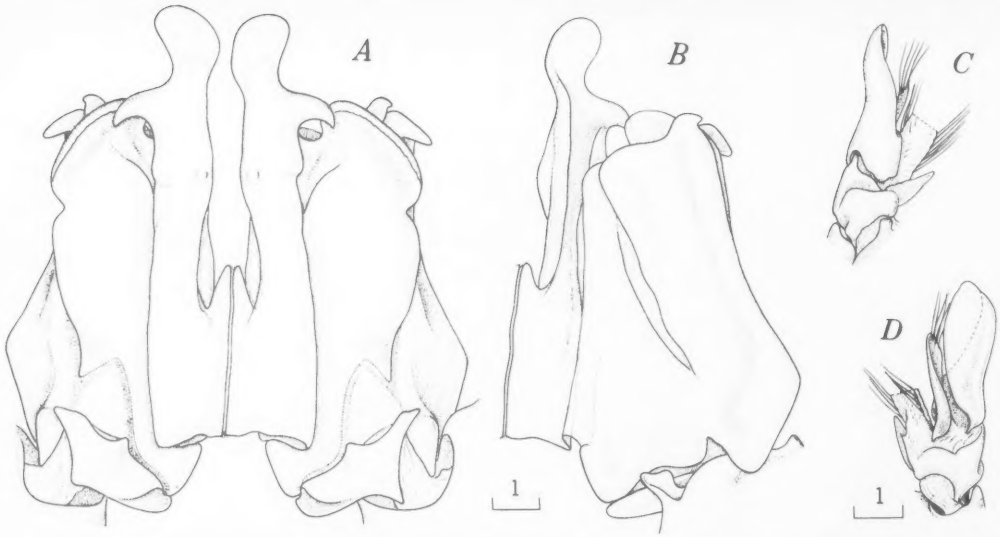

FIGURE 39.—*Pleoticus muelleri*, ♂ 20 mm cl, off Laguna Rocha, Uruguay. *A*, Petasma, dorsal view. *B*, Ventrolateral view of left half. *C*, Right appendices masculina and interna, lateral view. *D*, Mesial view.

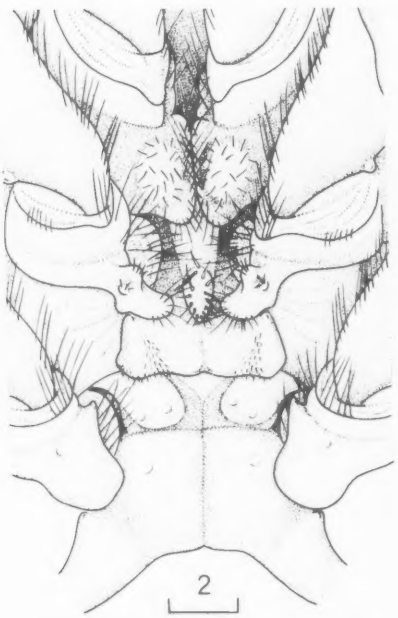

FIGURE 40.—*Pleoticus muelleri*, ♀ 43 mm cl, off Praia de Santana, Espírito Santo, Brazil. Thelycum, ventral view.

paired plates, each bearing pair of minute tubercles. Median plate of sternite XIII elevated laterally in ribs ending anteriorly in blunt horns, and armed with strong, blunt, setose median projection; latter flanked anteriorly by setose protuberances borne on articular membranes of fourth pereopods; sternite XII markedly convex, its strong transverse marginal ridge with deep median depression and blunt, lateral, posteriorly directed horns.

Color.–Pale yellow or yellowish red to tomato red (Boschi and Angelescu 1962); reddish orange of various shades in different areas of the body (Boschi 1963); wine-red in young from 50 mm tl through adulthood (Iwai 1973).

Maximum size.–Males: 37.5 mm cl; females: 58 mm cl.

Geographic and bathymetric ranges.–From off Praia de Santana, about 20°S, 40°W, Espírito Santo (data on label accompanying two specimens collected by Getulio de Souza Neiva), south to the northwestern portion of the Golfo de San Jorge, Comodoro Rivadavia (Figure 34). It occurs most

abundantly in littoral waters at depths between 2 and 20-30 m (Figure 9), and rarely as deep as 80-100 m (Angelescu and Boschi 1960; Boschi and Scelzo 1969a), and from near the shoreline to 0.5 km offshore, occasionally as far as 56 km (Angelescu and Boschi 1960). This species was reported by Iwai (1973) to range north to 21°36′S, the first record north of Ilha Santana, 22°25′S, Rio de Janeiro, where da Silva (1965) had reported a fishery for this shrimp. The specimens taken at Praia de Santana, Espírito Santo, about 178 km north of the locality where Iwai recorded the species, have confirmed the presence of *H. muelleri* beyond the state of Rio de Janeiro. The southernmost limit of the species given above is based on Boschi and Scelzo (1969a), who identified a number of large specimens caught in the Golfo de San Jorge at a depth of 80 m.

Affinities.–*Pleoticus muelleri* has its closest affinities with its Atlantic congener *P. robustus*, but it may be readily separated from it by its almost entirely glabrous body, long prosartema, which may overreach the midlength of the second antennular article, the absence of branchiostegal spines and the presence of orbital spines. Also it may be distinguished by the disposition of the submarginal carina, the posterior part of which is horizontal and situated far from the free ventral border of the carapace, instead of extending subparallel to that border as it does in all other species of this generic complex. The external genitalia of the two are also markedly different, as pointed out under *P. robustus*. In the petasma of *P. muelleri* the ventromedian lobule is cornified distally, terminates in a rounded to ovate platelike projection which bears at its base a spurlike projection, and the ventral costa is produced into a dorsally directed hook. The thelycum, in turn, exhibits paired short plates on the anterior part of sternite XIV, each bearing a pair of minute knobs, and also an exceedingly strong projection on the median plate of sternite XIII.

Spermatophore.–Compound spermatophore (Figure 41) consisting of broad geminate body with angular hump at about midlength, and bearing small pair of wings anterolaterally; also provided with large, highly sculptured midlateral flaps, and pair of broad, posterolateral flanges. Thick, opaque ventral wall of each spermatophore (Figure 42*A*) truncate, lacking anterior lobe, broadened and swollen at about midlength forming hump; area posterior to hump dorsally depressed, and strengthened by longitudinal ridge. Lateral wall mostly thick, concave, and insensibly continuous with wing anteriorly, merging with broad, subrectangular flap, and posteriorly bearing prominent longitudinal ridge parallel to that of ventral wall. Dorsomesial wall largely translucent, but heavily sclerotized and opaque mesially forming axial part of complex armature (Figure 42*C*). Latter bearing three transverse ribs: 1) anterior, forming arc, with one arm (ventral) strengthening ventral hump and another running across dorsomesial wall, then ending in foliaceous process; 2) intermediate, close to former, very strong, tonguelike, and deeply excavated; 3) posterior, forming shelf projecting inside lumen of sperm sac from dorsomesial wall. Wing short, broad, and flexible except for posterior thickening running along its entire length. Anterior part of flap broad, subrectangular, elevated in marginal

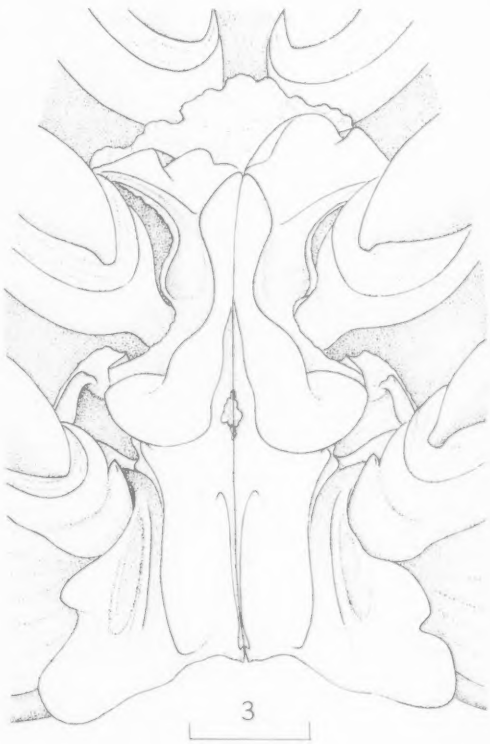

FIGURE 41.—*Pleoticus muelleri*. Compound spermatophore attached to female, ♀ 37 mm cl, Rawson, Chubut, Argentina (setae omitted).

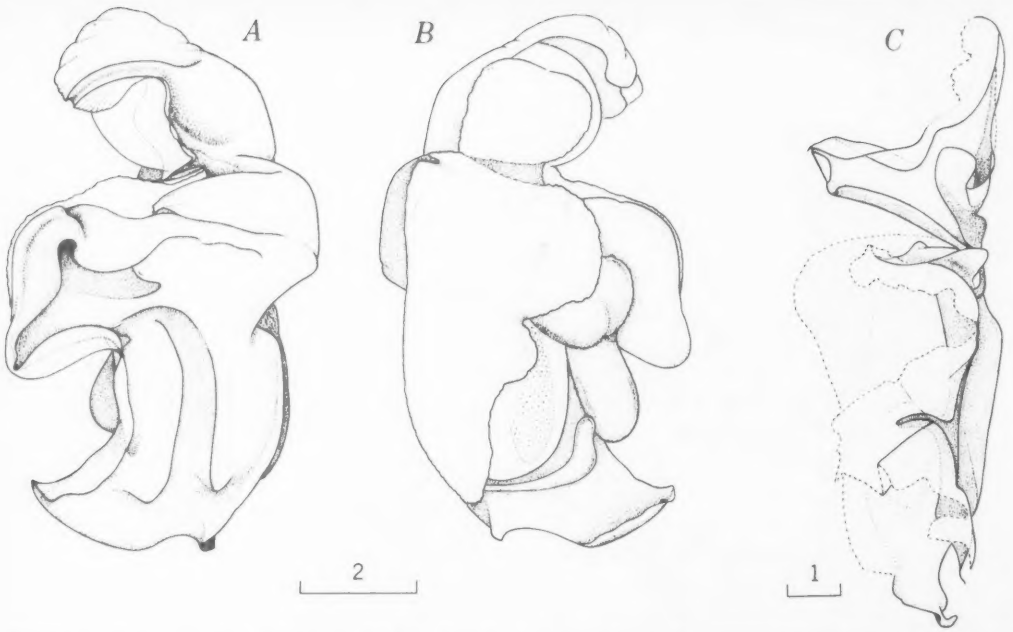

FIGURE 42.—*Pleoticus muelleri*, ♂ 37 mm cl, off Buenos Aires Province, Argentina. *A*, Right spermatophore dissected from terminal ampulla, ventrolateral view. *B*, Dorsomesial view. *C*, Left spermatophore dislodged from female, ♀ 59 mm cl, Puerto Madryn, Chubut, Argentina.

ridge continuous with hump; posterior part narrow, extending as flexible band joining flange. Flange short, with broad mesial base and sinuous lateral margin. Dorsal plate (Figure 42*B*) large, extending almost from anterior extremity of spermatophore to base of flange, and irregular in contour.

Compound spermatophore applied to thelycum much as it is in *P. robustus*. Anterior extremity of geminate body lying opposite female gonopores, with wings attached to ventral articular membranes of third pereopods. Ventral walls fused mesially while lateral walls diverge dorsally becoming affixed to sternite XIII, their lateral margins embracing mesial prominences of dorsal articular membranes of fourth pereopods. Strong humplike prominences projecting ventrally from sternite XIV, latter serving as place of attachment for broad anterior parts of flaps as well as for intimately fused dorsal plates. From humplike prominences, compound spermatophore sloping posterodorsally, and held in position by paired flanges affixed to ventral articular membranes of fifth pereopods.

The sperm is freed from each sac through an anterior rupture of dorsomesial wall, close to corresponding gonopores. The gelatinous substance which accompanies the sperm within the sperm sac may be observed covering the gonopores in Figure 41. Spermatophore-bearing females are not infrequent in collections; it seems that the spermatophores in this species as in *P. robustus*, which are also exceedingly large, become firmly anchored to the thelycum. According to Angelescu and Boschi (1960), the spermatophores in recently caught impregnated females are light green.

Postembryonic stages.–Boschi and Scelzo (1969a) prepared illustrated keys for the identification of larvae of the three more common Penaeidea in the waters off Argentina. These keys include diagnoses of protozoeae, mysis, and postlarvae of *P. muelleri* based both on specimens caught in plankton samples and others reared in the laboratory. Later, Scelzo and Boschi (1975) presented the results of their successful rearing of this shrimp from eggs spawned in the laboratory to

juveniles of an average total length of 21.3 mm. They stated that spawning generally took place the night following the capture of mature females, and eggs hatched between 12 and 24 h (according to the temperature) after being released. The young passed through 6 nauplii, 3 protozoeae, 3 mysis, and an undetermined number of postlarvae before becoming juveniles. The larval development was completed in 19-23 days at 19.0°-23.5°C and juveniles reached 21.3 mm (average) in 81 days after hatching. In more recent experiments, Boschi and Scelzo (1976) found that, at 24°C, *P. muelleri* attained an average of 61 mm tl and 2.7 g in 180 days after hatching. The studies mentioned above are the only ones that have been made on the development of any of the 12 species treated here.

Remarks.–Much of our knowledge of the morphology of this species is due to the study of Angelescu and Boschi (1960) and their subsequent contribution (Boschi and Angelescu 1962). These authors presented detailed accounts of the external and internal anatomy, and included outlines and a brief description of the "green" spermatophores on the female. In addition, they calculated the rate of growth of the species in Argentinian waters, studied the development of the testis and ovaries, and determined that the spawning season there extends from December to February (i.e., through the summer months). Furthermore, they found that it feeds on organic detritus as well as on small animals, such as sergestids and polychaetes, and plants.

Ecological notes.–Pleoticus muelleri is the only species of the genus which frequents shallow littoral waters; it even invades seawater channels and rías like those in the vicinity of Bahía Blanca, Buenos Aires, where, according to Boschi (1963), the "langostino" is trapped in weirs by the fishermen. Furthermore, this shrimp not only inhabits such shallow waters, but occurs in sufficient abundance to support commercial exploitation in many areas.

This species completes its entire life cycle in the sea but, as stated above, may frequent inshore waters of high salinity. It occupies tropical and subtropical waters off Brazil, where surface temperatures are as high as 25°-27°C during the warm months of the year, and 16°-17°C during the cold ones; farther south, off Argentina, it occurs in temperate waters where surface temperatures range between 10° and 23°C during the summer, and 5° and 10°C during the winter (Boschi 1964).

This shrimp lives on mud and sand bottoms.

Economic importance.–Pleoticus muelleri is taken commercially from Ilha Santana, Rio de Janeiro, to Punta Clara, Chubut. Significant catches, however, are made only from Santa Catarina to Punta Clara, and the largest fisheries are in Argentinian waters (Boschi 1964), between Punta Rasa (province of Buenos Aires) and Punta Clara, i.e., between 41° and 44°S. This species constitutes the largest percentage of the shrimp landings (which also include *Artemesia longinaris* Bate 1888) in Argentina.

Hadropenaeus New Genus

Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part].
Philonicus Bate 1888:273 [part].
Pleoticus Bate 1888:xii [part].
Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part].

Diagnosis.–Body stout, carapace proportionately short, integument moderately thick, firm. Rostrum short, not overreaching distal margin of first antennular article, deep, ventral margin pronouncedly convex; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than, that between first and second rostral teeth. Orbital and pterygostomian spines absent; postorbital, antennal, hepatic, and branchiostegal spines present. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac sulcus and carina absent, posthepatic and submarginal carinae absent. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous, fixed, lateral spines. Prosartema long, flexible. Antennular flagella longer than carapace, usually subcylindrical, ventral flagellum occasionally depressed. Mandibular palp two jointed, articles moderately broad, distal one as long as or slightly shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fifth pereopod subflagelliform and considerably longer than fourth. First pereopod with spine on basis,

ischium, and merus. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal spine). In males, petasma with ventral costa free from heavily sclerotized, platelike terminal part of ventrolateral lobule; ventromedian lobule broadly expanded distally. Endopod of second pereopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, not enclosing seminal receptacle. Pleurobranchia on somites IX to XIV; single rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII; podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

Hadropenaeus is an extremely homogeneous genus, the three known species being quite similar.

Type-species.–*Hymenopenaeus modestus* Smith 1885.

Etymology.–From the Greek *hadros,* stout, in combination with the generic name *Penaeus,* alluding to the comparatively short and thick carapace.

Gender.–Masculine.

List of species.–Amphi-Atlantic: *Hadropenaeus affinis* (Bouvier 1906b). Western Atlantic: *Hadropenaeus modestus* (Smith 1885). Indo-West Pacific: *Hadropenaeus lucasii* (Bate 1881).

Affinities.–The members of *Hadropenaeus* resemble those of *Pleoticus* (as here defined) in having the epigastric tooth separated from the first rostral by an interval equal to, or only slightly greater than, that between the first and second rostral teeth, in lacking both branchiocardiac and posthepatic carinae, and in possessing a petasma in which the ventral costa is free from the platelike, terminal part of the ventrolateral lobule. However, *Hadropenaeus* differs from *Pleoticus* (as well as from the other closely related genera except *Mesopenaeus*) in the proportionately higher carapace, in the shape of the rostrum which is short, deep, and possesses a strongly convex ventral margin, and in lacking submarginal carinae.

The members of this genus are closely allied to those of *Mesopenaeus.* They share a stout appearance, short, deep rostrum in which the ventral margin is convex, similar arrangement of the epigastric and rostral teeth, and they lack branchiocardiac sulci and carinae. Furthermore, the ventral flagellum, which is typically flattened in *Mesopenaeus,* is occasionally depressed in one species of *Hadropenaeus;* the depressed flagellum seemingly represents the first step in a process of specialization which progressed through the flattened ventral flagellum in *Mesopenaeus,* and culminated in the two lamellate flagella (both ventral and dorsal) in *Solenocera. Hadropenaeus,* in contrast to *Mesopenaeus,* lacks submarginal carinae and orbital spines; it possesses branchiostegal spines and, most significantly, exhibits a petasma in which the ventral costa is free from the terminal part of the ventrolateral lobule.

Key to Species of *Hadropenaeus*

1. Rostrum lacking conspicuous carina dorsal to adrostral one. Thelycum with median protuberance on sternite XIV high, projecting ventrally as far as posterior convexities of sternite XIII; latter with median ridge bearing large tooth anteriorly. Petasma with ventromedian lobule produced into distolateral projection 2

   Rostrum with conspicuous carina dorsal to adrostral one. Thelycum with median protuberance on sternite XIV low, not projecting ventrally as far as posterior convexities of sternite XIII; latter with median, keellike ridge lacking tooth anteriorly. Petasma with ventromedian lobule not produced into distolateral projection .... *H. lucasii*

2. Scaphocerite reaching distal end of antennular peduncle or overreaching it by not more than 0.1 of its own length. Prosartema extending only to distomesial extremity of first antennular article. Thelycum with median protuberance on sternite XIV projecting ventrally, and tooth of median keel of sternite XIII directed anteriorly. Petasma with distomesial projection of

ventromedian lobule directed mesially ..... *H. affinis*

Scaphocerite overreaching antennular peduncle by about 0.25 of its own length. Prosartema conspicuously overreaching distomesial margin of first antennular article. Thelycum with median protuberance on sternite XIV projecting anteriorly, and tooth of median keel of sternite XIII directed ventrally or posteriorly. Petasma with distomesial projection of ventromedian lobule directed distally .... *H. modestus*

Hadropenaeus affinis (Bouvier 1906)

Figures 9, 43, 44A, 45-49

Haliporus modestus Bouvier 1905a:980. [Not *Hymenopenaeus modestus* Smith 1885.]

Haliporus affinis Bouvier 1906b:4 [syntypes: 1 ♂ 2 ♀, 4 ♂ 4 ♀, 2 ♂ 2 ♀, MP; type-locality: off Cape Verde Is, 16°53′N, 25°10′W, 410-460 m, 29 July 1883, *Talisman* stn 116. Unrecorded number of syntypes from off Cape Verde Is, "100 m" from uncited *Talisman* station. 1 ♂, MCZ 7196, off Barbados, 188 m, 5 March 1879, *Blake* stn 273, 13°03′05″N, 59°36′18″W]. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:209. de Man 1911:7.

Hymenopenaeus affinis. Burkenroad 1936:104. Crosnier and Forest 1973:258, fig. 82b, 84, 94d.

Hymenopenaeus modestus. Bullis and Thompson 1965:5 [part]. [Not *Hymenopenaeus modestus* Smith 1885.]

Material

UNITED STATES—North Carolina: 2 ♀, UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, *Albatross III* stn 21-4. 3 ♂ 14 ♀, USNM, E of Port Fisher, 366 m, 15 November 1956, *Combat* stn 177. 2 ♂ 1 ♀, UNC-IMS, about 111 km SE of Cape Fear, 412-369 m, 23 June 1956, *Pelican* stn 75. South Carolina: 2 ♀, USNM, E of Cape I, 366 m, 20 April 1957, *Combat* stn 288. Florida: 1 ♀, USNM, off Hobe Sound, 302-285 m, 21 May 1968, *Gerda* stn 997. 1 ♀, USNM, off Boca Raton, 366 m, 29 March 1956, *Pelican* stn 17. 1 ♂, USNM, SE of Key Largo, 185 m, 22 January 1965, *Gerda* stn 452. 1 ♂, USNM, off Marathon, 201 m, 21 June 1967, *Gerda* stn 813. 1 ♂, USNM, S of Pine Is, 293-302 m, 25 February 1969, *Gerda* stn 1029. 2 ♀, USNM, NW of Double Headed Shot Cays, 223 m, 29 August 1967, *Gerda* stn 864. 1 ♂, USNM, NW of Charlotte Harbor, 366 m, 21 August 1970, *Oregon II* stn 11180.

BAHAMA ISLANDS—1 ♂, RMNH, NW of Matanilla Reef, 549-567 m, 1 July 1963, *Gerda* stn 179. 1 ♂, USNM, NW of Matanilla Reef, 466-417 m, 30 September 1967, *Gerda* stn 935. 1 ♀, USNM, NW of Matanilla Reef, 421 m, 3 February 1957, *Combat* stn 238. 1 ♀, USNM, N of Matanilla Reef, 393 m, 3 February 1957, *Combat* stn 237. 2 ♂, RMNH, W of Bimini Is, 452-474 m, 30 January 1964, *Gerda* stn 234. 3 ♀, USNM, SW of Bimini Is, 403-421 m, 30 January 1964, *Gerda* stn 233. 5 ♀, RMNH, off Gun Cay, 439-421 m, 29/30 January 1964, *Gerda* stn 232. 1 ♂, USNM, SW of Gun Cay, 312-348 m, 30 March 1964, *Gerda* stn 274. 1 ♂ 1 ♀, USNM, Santaren Channel, 384-366 m, 6 November 1960, *Silver Bay* stn 2468. 1 ♀, USNM, Santaren Channel, 412-220 m, 22 June 1967, *Gerda* stn 820. 1 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10849.

PUERTO RICO—3 ♀, USNM, Mona Passage, 366 m, 17 October 1963, *Silver Bay* stn 5190.

HAITI—1 ♀ juv, USNM, W of Anse d'Hainault, [?] 77 m, 2 July 1970, *Pillsbury* stn 1186.

LESSER ANTILLES—1 ♂, USNM, E of Rivière Pilote, Martinique I, 170-214 m, 9 July 1969, *Pillsbury* stn 907. 1 ♂, USNM, SE of Georgetown, St Vincent I, 165-201 m, 6 July 1969, *Pillsbury* stn 874. 1 ♂ syntype + 1 ♂, MCZ 7196, off South Point, Barbados, 188 m, 5 March 1879, *Blake* stn 273.

WESTERN CARIBBEAN—2 ♂ 4 ♀, USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, *Gerda* stn 954. 1 ♀, USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, *Gerda* stn 951. 1 ♂, UMML, Arrowsmith Bank, 252-293 m, 14 March 1968, *Pillsbury* stn 591. 2 ♂ 2 ♀, USNM, Arrowsmith Bank, 155-205 m, 15 March 1968, *Pillsbury* stn 598. 1 ♂, USNM, W of I de Providencia, 289-274 m, 4 February 1967, *Oregon* stn 6423.

MEXICO—Quintana Roo: 1 ♂ juv, UMML, SE of Isla Mujeres, 241-320 m, 10 September 1967, *Gerda* stn 893. 1 ♀, UMML, SE of Isla Mujeres, 210-366 m, 23 August 1970, *Gerda* stn 1286. 3 ♀, USNM, off Puerto de Morelos, 165-168 m, 10 September 1967, *Gerda* stn 899.

PANAMA—1 ♀, USNM, off Caribbean coast of Panama, 274 m, 5 July 1972, *Canopus*.

PORTUGAL—Cape Verde Is: 1 ♂ 2 ♀, 4 ♂ 4 ♀, 2 ♂ 2 ♀ syntypes, MP, 410-460 m, 29 July 1963, *Talisman* stn 116.

Description.–Body stout (Figure 43), integument moderately thick, firm. Carapace with restricted pubescent areas, setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth; minute, sparsely set setae on dorsum and hepatic region. Abdomen polished, almost entirely naked except for setae on posterior part of dorsal keel; telson and mesial ramus of uropod rather densely pubescent. Rostrum short, its length 0.20-0.25 that of carapace, falling short of distal margin of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex, with subapical concavity giving rise to saber-shaped tip; latter almost 0.4 length of rostrum. Rostral plus epigastric teeth 5-7 (mode 6; $N = 60$), base of third rostral tooth at level of orbital margin. Adrostral carina extending from orbital margin to ultimate tooth; more dorsal barely perceptible carina extending from second to ultimate rostral tooth; postrostral

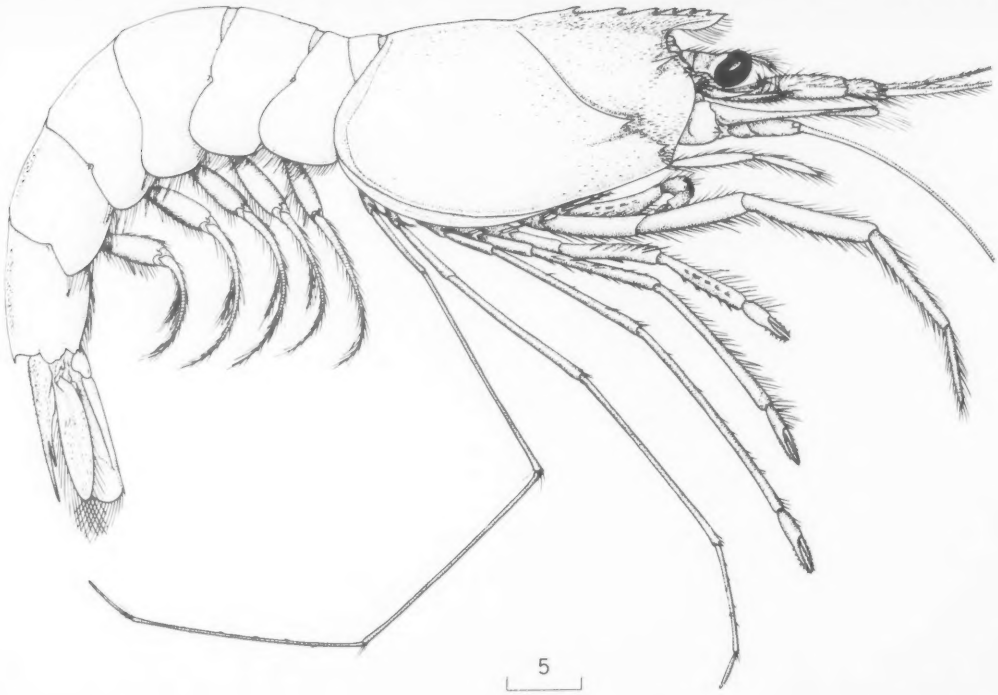

FIGURE 43.—*Hadropenaeus affinis*, ♀ 21.5 mm cl, Mona Passage, off Puerto Rico. Lateral view (third pereopod slightly raised).

carina ending immediately posterior to cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace, and close to postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye (Figure 44*A*) with basal article produced distomesially into pubescent, elongate scale; ocular peduncle moderately long, bearing minute tubercle; cornea broad, greatest diameter 1.5-1.9 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema falling short, or barely reaching, distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine, terminating in sharp spine; distolateral spine very slender and long, conspicuously surpassing proximal margin of second article. Antennular flagella long, length of dorsal flagellum 2.2 and 1.9 times carapace length in shrimp 8 and 23 mm cl, respectively; ventral shorter and broader than dorsal, gently tapering distally, and armed with marginal rows of long plumose setae. Scaphocerite extending to distal margin of antennular peduncle or exceeding it by less than 0.1 of its own length; lateral rib ending in slender spine, reaching to or very slightly beyond distal margin of lamella. Antennal flagellum long, although incomplete in all specimens examined, longest observed by me 3 times total length of shrimp. Mandibular palp (Figure 45*A*) moderately broad, distal article slightly shorter than basal. First maxilliped as illustrated (Figure 45*B*); rudimentary arthrobranchia of corresponding somite VII situated near its base (Figure 45*c*-*c*^{1}). Third maxilliped exceeding antennular peduncle by length of dactyl and half or as much as entire length of propodus.

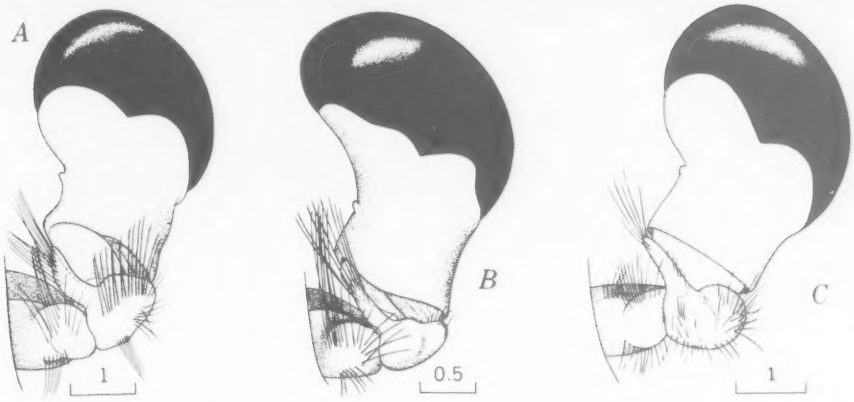

FIGURE 44.—Eyes. *A, Hadropenaeus affinis,* ♀ 21 mm cl, southeast of Cape Lookout, N.C. *B, Hadropenaeus modestus,* ♂ 11 mm cl, southwest of Dry Tortugas, Fla. *C, Hadropenaeus lucasii,* ♀ 18 mm cl, Pailolo Channel, Hawaiian Islands.

First pereopod, stoutest of all, reaching at least basal 0.65 length of carpocerite, and, at most, exceeding it by tip of dactyl. Second pereopod moderately stout, extending to distal end of carpocerite or exceeding it by as much as entire propodus. Third pereopod surpassing antennular peduncle by length of dactyl or by entire propodus. Fourth pereopod exceeding antennular peduncle by dactyl and 0.2-0.6 length of propodus; length of dactyl about 0.4 that of propodus; length of carpus about 1.25 times that of merus. Fifth pereopod slender and long, overreaching antennular peduncle at least by length of dactyl and propodus, or by as much as their length and almost 0.3 length of carpus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third (occasionally third, fourth), and fifth. First pereopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and small one near midlength of mesial margin of merus. Second pereopod with long spine on basis. Coxa of fourth and fifth pereopods in males armed with anterior spine. Coxa of fifth pereopod in females produced mesially into short plate bearing sharp spine anteromesially.

Abdomen with middorsal keel from fourth through sixth somites; low rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at pos-

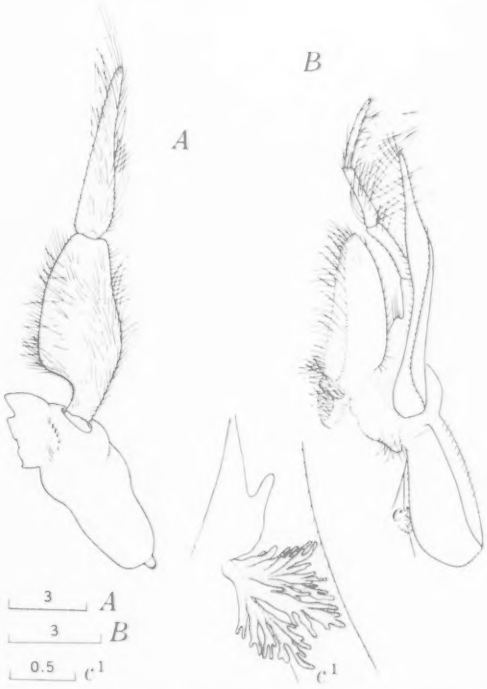

FIGURE 45.—*Hadropenaeus affinis,* ♀ 21.5 mm cl, southeast of Cape Lookout, N.C. *A,* Mandible. *B,* First maxilliped. *c,* Arthrobranchia. *c*¹, Enlargement of *c* (all from left side).

terior end of keel, and minute spine at posteroventral angles. Telson (Figure 46*A*) pubescent except for median sulcus and terminal portion; sulcus deep anteriorly, increasingly shallow posteriorly, ending before reaching lateral spines; spines long, their length 1.6-1.9 basal width of terminal portion; latter long, length 3.5-4.5 times basal width; mesial ramus of uropod barely overreaching apex of telson, or exceeding it by about 0.15 of its own length; lateral ramus distinctly surpassing mesial, and armed with small, distolateral spine, projecting beyond contiguous distal margin of ramus.

Petasma (Figure 47*A, B*) cincinnulate along proximal 0.65 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, with border adjacent to ventral costa bearing emargination delimiting basal part from subovate terminal part; latter strongly inclined toward, and partially covered by, ventromedian lobule, and armed with minute spinules along ventral margin; ventral costa with distal part free from contiguous plate, bent outward and bearing spinules on distalmost margin.

Appendix masculina (Figure 47*C, D*) with proximal part broad, strongly produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, strongly turned laterally, with apical portion armed with tuft of long setae; appendix interna shorter than appendix masculina, narrow, sinuous, and bearing apical tuft of long setae. Ventrolateral spur large, subelliptical to paddlelike.

Thelycum (Figure 48*A, B*) with median protuberance on sternite XIV subconical, its apical portion directed anteriorly or ventrally and produced into spinelike projection; protuberance situated distinctly posterior to prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal median keel on sternite XIII produced anteriorly into anteriorly directed blunt tooth, its cephalic margin concave, its posterior margin convex.

Photophores.–Paired photophores situated on posterolateral margins of sternites X through XIII just mesial to coxae of first four pairs of pereopods.

Color.–Color notes made by Lipke B. Holthuis (pers. commun.) on a male caught southeast of Georgetown, St. Vincent Island, at *Pillsbury* stn 874, state that the shrimp was "uniformly red, with darker bands parallel to the posterior margins of the abdominal terga."

The following description is based upon a freshly caught specimen observed by me during a 1969 cruise of *Oregon II*, south of Great Inagua Island, Bahamas. Body translucent pinkish orange, with gnathal appendages, and pereopods reddish orange. Carapace with milky white subtriangular patch lying immediately dorsal to hepatic spine, its broad base abutting cervical sulcus; small, middorsal, diamond shaped marking (formed by white lines) just posterior to midlength of carapace; anterolateral sides of marking continuing posterolaterally in dorsalmost arm of transverse, strongly sinuous, opaque white, narrow band; ventral arm of U-shaped dorsal portion of band extending anteriorly to cervical sulcus,

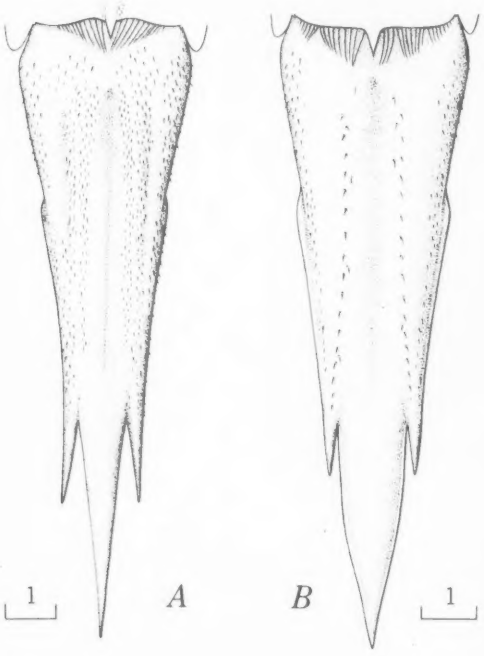

FIGURE 46.—Telsons. *A*, *Hadropenaeus affinis*, ♀ 20 mm cl, southwest of Bimini Islands, Great Bahama Bank. *B*, *Hadropenaeus modestus*, ♀ 19 mm cl, west of Isla de Providencia, western Caribbean.

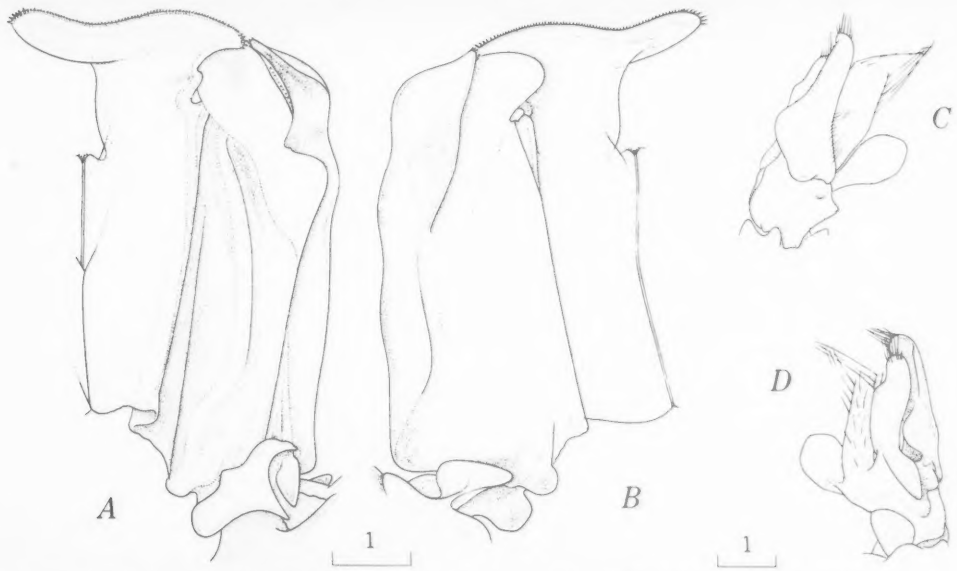

FIGURE 47.—*Hadropenaeus affinis*, ♂ 16 mm cl, about 11 km southeast of Cape Fear, N.C. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

there turning caudad reaching posterior end of hepatic sulcus; middorsal patch of white specks extending from posterior sides of diamond to posterior margin of carapace. First five abdominal somites with reddish orange band along posterior margin of tergum, band broader dorsally, tapering posteroventrally to level of articular knob, then extending anteroventrally to about mid-

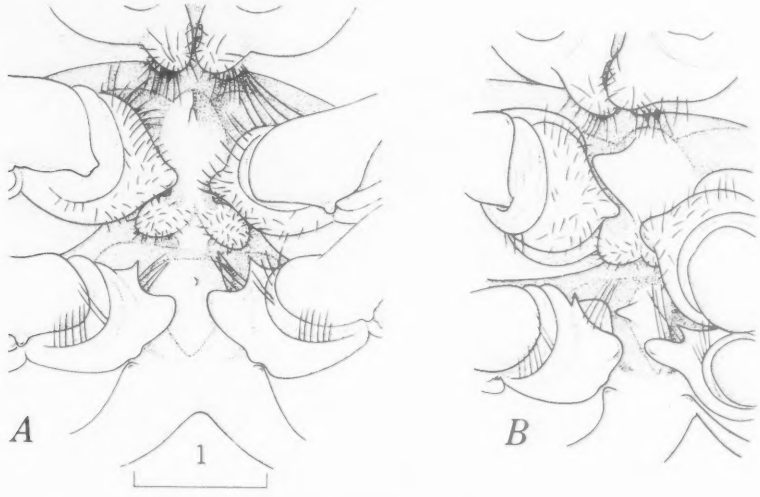

FIGURE 48.—*Hadropenaeus affinis*, ♀ 19 mm cl, east of Cape Island, S.C. *A*, Thelycum, ventral view. *B*, Ventrolateral view.

length of ventral margin of pleuron and from there anteriorly to ventral angle of latter.

Maximum size.–Males: 15 mm cl, about 66 mm tl; females: 23 mm cl, about 82 mm tl.

Geographic and bathymetric ranges.–In the western Atlantic: from off Cape Lookout, N.C. (34°15′N, 75°58′W), southward to the Straits of Florida, in the northeastern part of the Gulf of Mexico (northwest of Charlotte Harbor, Fla.), and throughout the Caribbean. In the eastern Atlantic: off Cape Verde Islands (Figure 49). This species has been found at depths between 165 and 570 m (Figure 9), with one dubious record from Haiti at 77 m.

Affinities.–Hadropenaeus affinis, which is amphi-Atlantic, and *H. modestus,* found only in the western Atlantic, are closely allied, but can be distinguished by the characters presented in Table 1.

Burkenroad (1936), for unexplained reasons, expressed doubt that *H. affinis* is different from *H. modestus,* an opinion apparently shared by Bullis and Thompson (1965) who recognized only *H. modestus* in their western Atlantic collections. I have examined part of their material and found that it also includes *H. affinis.* On the basis of the original description of *H. modestus* (Smith 1885), Bouvier (1906b) distinguished *H. affinis* from the former species by six features. I have found that two of them are diagnostic: the relative length of the scaphocerite, and the ratio length of dactyl/length of propodus of the fourth pereopod (see Table 1). The number of rostral teeth is not 7 in *H. modestus* as Smith indicated, but 6 in all specimens I have examined, the number usually possessed by *H. affinis.* The relative length of the antennular flagella, which Bouvier indicated was greater in *H. affinis,* varies within a given length of carapace, and may be the same in animals of the two species, e.g., 1.9 times carapace length in shrimp 23 mm cl. The carpus of the fourth pereopod is longer than the merus in both species, and not shorter in *H. modestus,* as Bou-

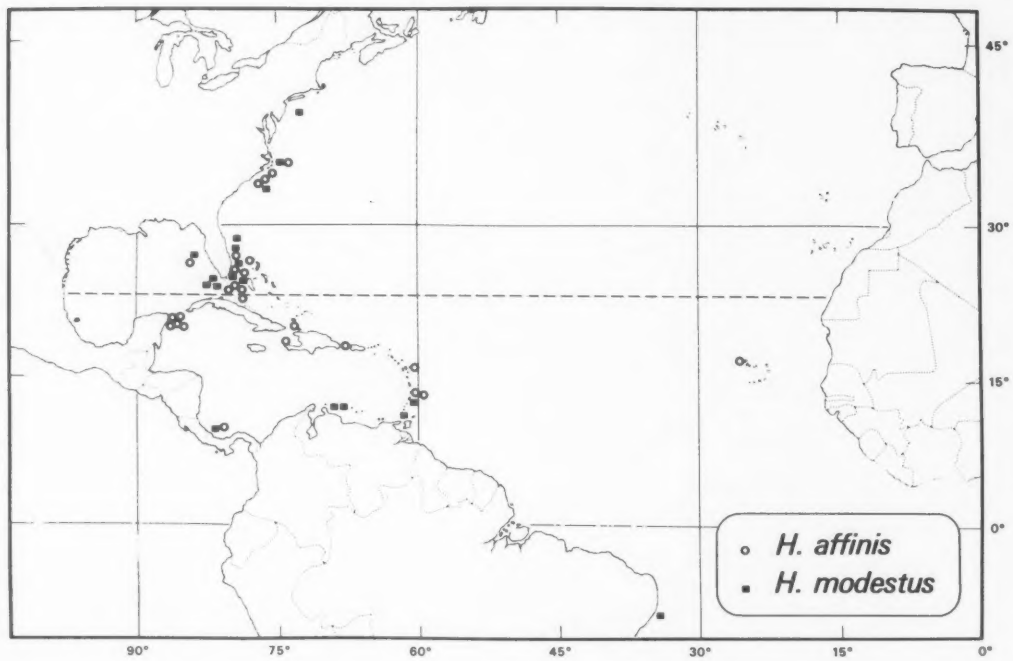

FIGURE 49.—Ranges of *Hadropenaeus affinis* and *Hadropenaeus modestus* based on published records and specimens personally examined.

TABLE 1.—Characteristics distinguishing *Hadropenaeus affinis* from *H. modestus*.

Feature	*H. affinis*	*H. modestus*
Scaphocerite	Reaching distal end of antennular peduncle or surpassing it by less than 0.10 of its own length	Surpassing antennular peduncle by as much as 0.25 of its own length
Prosartema	Extending only to distomesial extremity of first antennular article	Conspicuously overreaching distomesial extremity of first antennular article
Fourth pereopod	Extending farther anteriorly than third pereopod; surpassing antennular peduncle by as much as length of dactyl and that of propodus; length of dactyl less than 0.5 that of propodus	Not extending so far anteriorly as third pereopod, reaching at most distal end of first antennular article; length of dactyl greater than 0.5 that of propodus
Coxa of fifth pereopod in females	Bearing strong anteromesial spine	Lacking anteromesial spine in adult, occasionally with inconspicuous one in juvenile
Terminal portion of telson	Long, length 3.5-4.5 its basal width	Short, length 2.5-3.3 its basal width
Telsonic spines	Long, length more than 1.5 basal width of terminal portion of telson	Short, length not more than basal width of terminal portion of telson
Telsonic pubescence	Extensive, lacking on terminal portion	Limited to paired rows flanking median sulcus and lateral margins
Petasma	Ventromedian lobule with distomesial projection directed mesially; distal part of dorsolateral lobule subelliptical	Ventromedian lobule with distomesial projection directed distally; distal portion of dorsolateral lobule subrectangular
Thelycum	Protuberance of sternite XIV mammiform, with apical part directed ventrally; median keel of sternite XIII produced into anteriorly directed blunt tooth	Protuberance of sternite XIV subovate, with apical part directed anteriorly; median keel of sternite XIII produced into ventrally or posteriorly directed blunt tooth

vier calculated from Smith's erroneous data. Finally, the lateral ramus of the uropod is similar in shape in the two species, its distal part truncate and turning gently proximomesially. The descriptions of both the petasma and the thelycum of *H. affinis* presented by A. Milne Edwards and Bouvier (1909), together with the two diagnostic characters mentioned above, adequately diagnose the species.

Specimens from various localities in the western Atlantic exhibit differences in the shape of coxal spine of the fifth pereopod which varies from nearly blunt to sharply acute. Also in the sculpture of the thelycum, the apical portion of the protuberance on sternite XIV may be directed anteriorly or ventrally. The observed variations, however, intergrade and, furthermore, in some specimens the shape of the spine and the direction of the protuberance are identical to those exhibited by the syntypic material.

Remarks.–The numerous records cited above are the first from the western Atlantic since Bouvier (1906b) cited a syntypic male from off Barbados (*Blake* stn 273) in the original description of the species, and A. Milne Edwards and Bouvier (1909) recorded an additional juvenile male, which had been taken with the syntype.

The presence of photophores on the thoracic sternites of this species is revealed here for the first time. The photophores were observed in a recently caught specimen obtained from the *Oregon II*, south of Great Inagua, Bahamas; they are similar to those described by Burkenroad (1936) in *Hymenopenaeus debilis*.

Hadropenaeus modestus (Smith 1885)

Figures 9, 44B, 46B, 49-52

Hymenopenaeus modestus Smith 1885:183 [holotype: ♀ USNM 7267; type-locality: off Bethany Beach, Del., 38°31'N, 73°21'W, 156 fm (285 m), *Fish Hawk* stn 1047]. Burkenroad 1936:104. Bullis and Thompson 1965:5 [part]. Crosnier and Forest 1973:259.

Haliporus modestus. Bouvier 1905a:980; 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909: 209. de Man 1911:7. Fowler 1912:543.

Material

UNITED STATES—Delaware: ♀ holotype, USNM 7267, off Bethany Beach, 285 m, 10 October 1881, *Fish Hawk* stn 1047. North Carolina: 1 ♂, USNM, SE of Cape Lookout, 348-384 m, 13 November 1956, *Combat* stn 171. 1 ♂, USNM, SE of Cape Lookout, 329 m, 1 February 1972, *Oregon II* stn 11762. 1 ♂ 2 ♀, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, *Silver Bay* stn 1693. Georgia: 1 ♀, USNM, off Ossabaw, 238 m, 21 January 1972, *Oregon II* stn 11720. Florida: 1 ♂, USNM, off Melbourne Beach, 329 m, 31 January 1957, *Combat* stn 226. 1 ♀, USNM, off Hobe Sound, 302-285 m, 21 May 1968, *Gerda* stn 997. 1 ♀, AMNH, 21 km E of Boynton, 320-266 m, 17 May 1948, Burey. 1 ♀, RMNH, off Miami, 418 m, 27/28 August 1962, *Gerda* stn 53. 1 ♀, RMNH, E of Old Rhodes Key, 146 m, 25 September 1964, *Gerda* stn 427. 2 ♀, USNM, off Elliott Key, 194-187 m, 25 August 1967, *Gerda* stn 857. 1 ♀, UMML, NE of Key Largo, 265-275 m, 24 January 1964, *Gerda* stn 229. 3 ♂ 3 ♀, USNM, SE of Key Largo, 185 m, 22 January 1965, *Gerda* stn 452. 1 ♀, RMNH, SW of Marquesas Keys, 188-199 m, 28 November 1964, *Gerda* stn 432. 1 ♂, USNM, SW of Marquesas Keys, 177-229 m, 26 April 1969, *Gerda* stn 1087. 1 ♂, UMML, S of Dry Tortugas Is, [?] 68 m, 12 April 1965, *Gerda* stn 564. 1 ♀, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 1 part of carapace,

USNM, NW of Charlotte Harbor, 274 m, 22 August 1970, *Oregon II* stn 11181.

BAHAMAS—2 ♀, RMNH, W of Gun Cay I, 458-531 m, 30 January 1964, *Gerda* stn 242. 1 ♀, RMNH, N of Double Headed Shot Cays, 443 m, 27 January 1965, *Gerda* stn 483.

LESSER ANTILLES—3 ♂ 1 ♀, USNM, E of The Grenadines, 357-658 m, 4 July 1969, *Pillsbury* stn 861.

WESTERN CARIBBEAN—1 ♀, USNM, W of Old Providence I, 549 m, 12 September 1957, *Oregon* stn 1918.

PANAMA—1 ♀, USNM, Golfo de los Mosquitos, 274-293 m, 31 May 1962, *Oregon* stn 3597.

VENEZUELA—1 ♀, USNM, E of Península de Paraguaná, 366 m, 4 October 1963, *Oregon* stn 4421. 1 ♂, USNM, off San Juan de los Cayos, 384 m, 9 October 1963, *Oregon* stn 4440.

TRINIDAD - TOBAGO—2 ♂, USNM, NW of Tobago, 146 m, 2 July 1969, *Pillsbury* stn 848.

BRAZIL—Alagoas: 1 ♂, BMNH, off Barra Grande, 10 September 1873, *Challenger* stn 122-122C.

Description.–Carapace (Figure 50) finely pubescent; setae dense and long on base of rostrum, gastric, and epigastric regions; small setae on cardiac region, and minute ones sparsely set on hepatic and branchial regions; abdomen polished, and almost entirely naked except for setae on posterodorsal keel; pubescence of telson as in Figure 46*B*. Rostrum short, its length 0.25-0.30 that of carapace, reaching little beyond midlength of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex but with subapical concavity giving rise to saber shaped tip; latter 0.3-0.4 length of rostrum. Rostral plus epigastric teeth 6, apex of third rostral tooth or fourth tooth at level of orbital margin. Adrostral carina extending from orbital margin to ultimate tooth; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly in ventrally inclined short shelf. Postorbital spine, longest of four lateral spines on carapace, situated dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace at base of postrostral carina; cervical carina sharp; hepatic sulcus almost horizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44*B*).

Antennular peduncle length equivalent to about 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine; latter slender and long; flagella long, length of dorsal flagellum 1.9 cl in shrimp 23 mm cl, proximal portion of flagellum slightly broader than subfiliform distal portion; ventral flagellum slightly shorter and broader than dorsal, gently tapering distally, and bearing long, marginal plumose setae. Scaphocerite overreaching antennular peduncle by as much as 0.2 of its own length, gently tapering from base to narrow distal portion; lateral rib ending in long, slender spine, barely or conspicuously overreaching distal margin of lamella. Antennal flagellum long, at least 3 times total length of shrimp. Mandibular palp with distal article slightly shorter than basal and almost reaching or barely overreaching distal margin of carpocerite. Third maxilliped surpassing antennular peduncle by length of dactyl and 0.2-0.5 length of propodus.

First pereopod stout, reaching between midlength and distal end of carpocerite. Second pereopod moderately stout, extending almost to distal end of carpocerite or overreaching it by not more

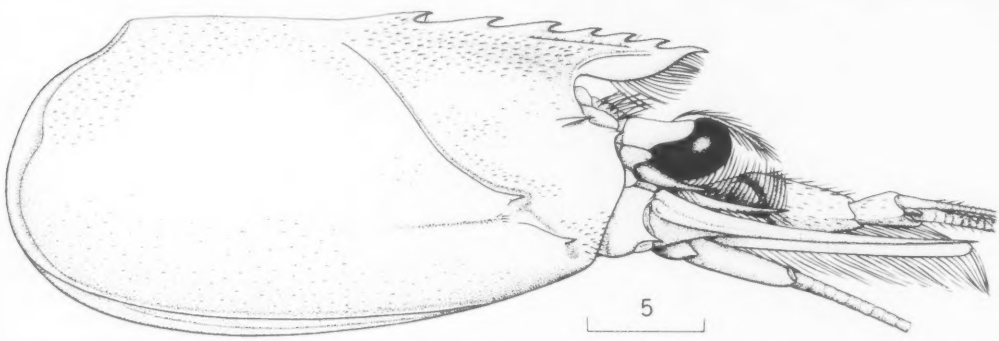

FIGURE 50.—*Hadropenaeus modestus*, 19 mm cl, west of Isla de Providencia, western Caribbean. Cephalothorax, lateral view.

than 0.5 length of dactyl. Third pereopod rather slender, exceeding antennular peduncle by tip or by entire length of dactyl. Fourth pereopod very slender, shorter than third, surpassing carpocerite by tip or by entire length of dactyl; length of dactyl 0.65-0.75 that of propodus; length of carpus about 1.1 times that of merus. Fifth pereopod very slender and long, overreaching antennular peduncle at least by length of dactyl and propodus, and at most by their length and 0.2 length of carpus. Order of pereopods in terms of their maximal anterior extensions; first, second, fourth, third, and fifth. First pereopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and rather minute one near midlength of mesial margin of merus. Second pereopod with long spine on basis. Coxa of fourth and fifth pereopods in males armed with anterior spine. Coxa of fifth pereopod in females mesially produced into short plate, lacking spine on anteromesial margin; minute spine present in young.

Abdomen with high, sharp, median keel from fourth through sixth somites, low, rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at posterior end of keel, and minute spine on posteroventral angles. Telson (Figure 46*B*) with median sulcus deep anteriorly, disappearing well anterior to terminal portion; fixed lateral spines relatively short, their length 0.7-0.8 basal width of terminal portion; latter broad, length 2.5-3.3 times basal width; mesial ramus of uropod overreaching apex of telson by as much as 0.2 of its own length; lateral ramus conspicuously surpassing mesial, and armed with small distolateral spine, slightly projecting beyond contiguous distal margin of ramus.

Petasma (Figure 51*A*, *B*) cincinnulate along proximal 0.6 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection, and with terminal margin spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate with border undulate adjacent to ventral costa, its terminal portion subrectangular, strongly inclined toward, and partially covered by, ventro-

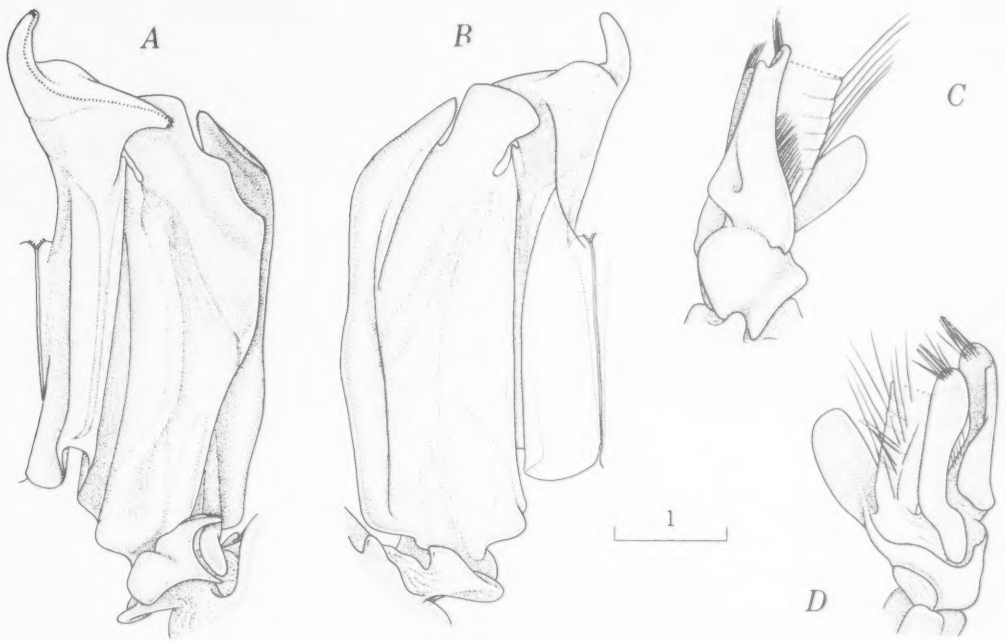

FIGURE 51.—*Hadropenaeus modestus*, ♂ 16.5 mm cl, southeast of Cape Fear, N.C. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

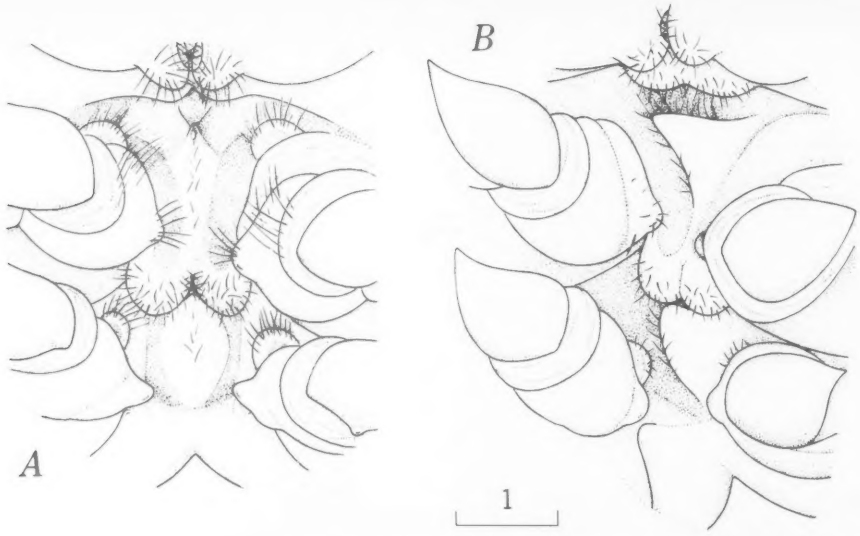

FIGURE 52.—*Hadropenaeus modestus*, holotype ♀ 8 mm cl, off Bethany Beach, Del. *A*, Thelycum, ventral view. *B*, Ventrolateral view.

median lobule; ventral costa with distal part free from contiguous plate, bent outward and bearing minute spinules on distalmost margin.

Appendix masculina and appendix interna together with ventrolateral spur (Figure 51*C*, *D*) similar to those of *H. affinis* (see above).

Thelycum (Figure 52*A*, *B*) with median protuberance on sternite XIV pyriform or subovate, its apical portion directed anteriorly, and lying between prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal, high, median keel on sternite XIII produced anteriorly into ventrally or posteroventrally directed blunt tooth, with anterior margin straight or convex and posterior margin concave.

Maximum size.–Females: 19.5 mm cl; males: 17.5 mm cl.

Geographic and bathymetric ranges.–Off Delaware Bay (38°31′N, 73°21′W), to the Straits of Florida, and in the Gulf of Mexico, northwest of Charlotte Harbor, Fla.; also from the Bahamas, throughout the Caribbean to off Barra Grande (about 9°10′S, 34°52′W), Brazil (Figure 49). This species has been recorded at a depth range of about 150-550 m (Figure 9).

Affinities.–Hadropenaeus modestus may be readily distinguished from its close relative *H. affinis* by the characters included in Table 1.

Remarks.–I have examined the holotype of *H. modestus* and found that, contrary to the data presented by Smith (1885), it possesses 6 rostral teeth (including epigastric), not 7, and that the merus of the fourth pereopod is only 6.5 mm long, not 7.5 mm. Therefore the carpus, which is 7.2 mm long, is not shorter than the merus, but about 1.1 times the length of the latter. These incorrect statements led Bouvier (1906b) to point out differences in the rostral armature and relative length of the carpus between *H. modestus* and *H. affinis* which do not exist.

Hadropenaeus modestus is newly reported here in the Caribbean and the Atlantic off northeast South America. The locality record from off Barra Grande, Brazil, is based on a single male taken during the voyage of the *Challenger* (1873-76). On the label accompanying this specimen is "Barra Grande, Brazil, *Challenger*." Although there are several towns in Brazil bearing the name Barra Grande, the locality referred to above must be that in the State of Alagoas, because according to Tizard et al. (1885), the white cliffs of Barra Grande could be seen from *Chal-*

lenger stn 122, 122A, 122B, and 122C, which are between 9°5′ and 9°10′S. This specimen has not been recorded in the literature previously—probably because it is a juvenile, not readily identifiable.

Hadropenaeus lucasii (Bate 1881)

Figures 9, 16, 44C, 53-55

Solenocera lucasii Bate 1881:185 [holotype: ♀, BMNH, off Kai Is, south of New Guinea, 5°49′15″S, 132°14′15″E, 140 fm (256 m), 26 September 1874, *Challenger* stn 192]. [Not *Solenocera lucasii*. Miers 1884:15. Rathbun 1906:904, pl. 20, fig. 9.]

Philonicus lucasii. Bate 1888:277, pl. 42, fig. 4. ? Thomson 1904:254.

Pleoticus lucasii. Bate 1888:939.

Haliporus modestus. Rathbun 1906:905, pl. 20, fig. 4. [Not *Hymenopenaeus* [*Hadropenaeus*] *modestus* Smith 1885.]

Haliporus lucasi. Bouvier 1908:80.

?*Haliporus malhaensis* Borradaile 1910:258, fig. 2 [type not extant; type-locality: off Saya de Malha, Indian Ocean, 145 fm (265 m)]. de Man 1911:7.

Haliporus lucasii. de Man 1911:7.

Hymenopenaeus lucasii. Burkenroad 1936:104. Anderson and Lindner 1945:289. Kubo 1949: 213, fig. 8 B[1], 20 Q, 27 K-N, 66 O, P, 72 C, I, 80 H, 91, 92 A, C.

?*Hymenopenaeus lucassi*. Ramadan 1938:57.

Hymenopenaeus lucasi. Crosnier and Forest 1973: 256, fig. 83a.

Material

HAWAII—6 ♂ 5 ♀, USNM, Pailolo Channel, 271-223 m, 23 July 1902, *Albatross* stn 4101. 1 ♂ 1 ♀, USNM, Pailolo Channel, 223-241 m, 23 July 1902, *Albatross* stn 4102. 1 ♀, USNM, Pailolo Channel, 241-258 m, 23 July 1902, *Albatross* stn 4103. 1 ♀, USNM, N coast of Maui I, 369-402 m, 21 July 1902, *Albatross* stn 4081. 3 ♂ 10 ♀, USNM, NW coast of Maui I, 214 m, 16 November 1968, *Townsend Cromwell* stn 40-43. 4 ♀, USNM, NW coast of Maui I, 218 m, 17 November 1968, *Townsend Cromwell* stn 40-48. 4 ♂ 12 ♀, USNM, NW coast of Maui I, 218 m, 17 November 1968, *Townsend Cromwell* stn 40-49. 1 ♂ 12 ♀, USNM, NW coast of Maui I, 216-232 m, 28 April 1968, *Townsend Cromwell* stn 36-11. 1 ♂ 16 ♀, USNM, Kaiwi Channel, 177-183 m, 5 May 1968, *Townsend Cromwell* stn 36-26. 3 ♀, USNM, S coast of Oahu I, 538-470 m, 6 May 1902, *Albatross* stn 3920. 2 ♀, USNM, N coast of Oahu I, 176-201 m, 12 July 1972, *Townsend Cromwell* stn 59-3. 2 ♂, USNM, NW coast of Oahu I, 395-459 m, 25 July 1902, *Albatross* stn 4121. 1 ♂ 1 ♀, USNM, vicinity of Laysan I, 271-298 m, 16 May 1902, *Albatross* stn 3938. 1 ♂, USNM, vicinity of Laysan I, 364-177 m, 19 May 1902, *Albatross* stn 3947.

NEW GUINEA—1 ♀ holotype, BMNH, off Kai Is, 256 m, 26 September 1874, *Challenger* stn 192.

REPUBLIC OF MALDIVES—1 ♀, BMNH, off Maldive Is, 256-293 m, 4 April 1934, The John Murray Expedition stn 153.

MADAGASCAR—1 ♂, USNM, NW of Baie du Currier, 350-360 m, 15 September 1972, A. Crosnier.

Description.–Carapace (Figure 53) with restricted pubescent areas: setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth. Abdomen polished and naked; telson with rows of minute setae flanking median sulcus and lateral margins; mesial ramus of uropod sparsely pubescent. Rostrum short, its length 0.30-0.35 that of carapace, reaching to, or almost to, distal margin of first antennular article, horizontal, with dorsal margin straight and ventral margin strongly

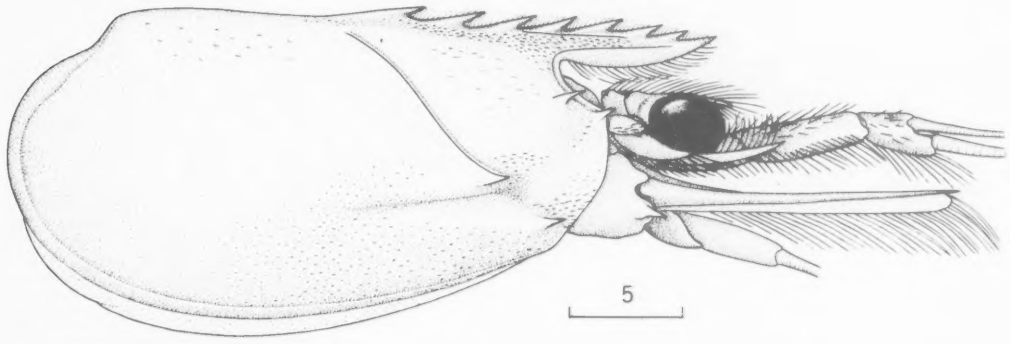

FIGURE 53.—*Hadropenaeus lucasii*, ♀ 18.5 mm cl, northwest coast of Maui, Hawaiian Islands. Cephalothorax, lateral view.

convex; tip about 0.2 length of rostrum. Rostral plus epigastric teeth 6-8 (mode 7; percentage distribution: 6-13.3, 7-83.3, 8-3.3; $N = 60$); third rostral tooth usually situated at level of orbital margin. Adrostral carina extending from orbital margin to base of ultimate tooth, and shorter, more dorsal, conspicuous carina extending from second rostral tooth to penultimate; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, usually more slender than middorsal teeth on carapace, and located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just anterior to midlength of carapace, near postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, originating almost at level of dorsal extremity of cervical sulcus, shallow and inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44*C*).

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter very slender and long, considerably surpassing proximal margin of second article. Antennular flagella long and considerably unequal in length, dorsal 1.85 times carapace length and ventral 1.30 in shrimp 12.5 mm cl, and 1.35 and 0.90, respectively, in shrimp 27 mm cl; dorsal flagellum subcylindrical, ventral subcylindrical to depressed. Scaphocerite reaching to distal margin of antennular peduncle or overreaching it by as much as 0.15 of its own length; lateral rib ending in spine reaching to, or slightly beyond, distal margin of lamella. Antennal flagellum long, although incomplete in all specimens, longest observed 3 times total length of shrimp. Mandibular palp with article as long as or slightly shorter than basal, reaching between midlength and distal 0.35 of carpocerite. Third maxilliped reaching to midlength of third antennular article or overreaching it by as much as 0.5 length of propodus; length of dactyl 0.75 that of propodus.

First pereopod, stoutest of five, reaching between midlength and distal 0.15 of carpocerite. Second pereopod extending to distal end of carpocerite or overreaching it by as much as entire length of dactyl. Third pereopod overreaching antennular peduncle by 0.5 length of dactyl or by

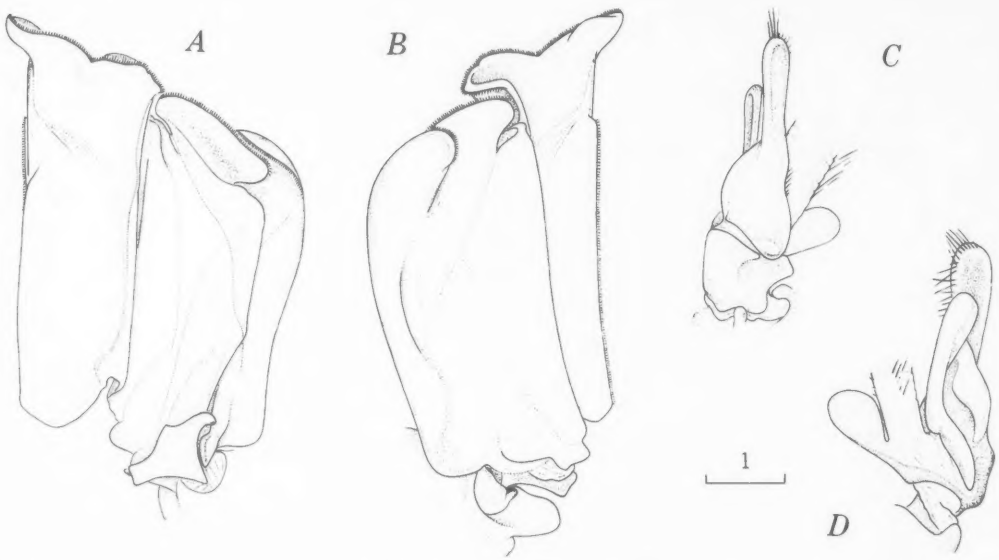

FIGURE 54.—*Hadropenaeus lucasii*, ♂ 13 mm cl, Pailolo Channel, Hawaiian Islands. *A*, Petasma (partly bent laterally), dorsal view of right half. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsolateral view. *D*, Ventromesial view.

as much as entire propodus. Fourth pereopod exceeding carpocerite by almost length of dactyl and sometimes by as much as length of dactyl and 0.15 that of propodus. Fifth pereopod reaching beyond antennular peduncle by length of dactyl and 0.6 to entire length of propodus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First pereopod bearing very long spine on distomesial extremity of basis, long one on that of ischium, and relatively small spine almost at midlength of merus. Second pereopod with long spine on basis. In female, coxa of third pereopod produced mesially into rather short densely setose plate; coxa of fourth pereopod bearing narrow plate. In both sexes, coxa of fourth and fifth pereopods bearing conspicuous anterior spine.

Abdomen with strong middorsal carina from third through sixth somites, carina rounded on third, forming keel from fourth posteriorly; posterodorsal margin of third, fourth, and fifth with long median incision; sixth somite length about 1.3 times maximum height, bearing sharp spine at posterior end of keel and minute spines at posteroventral angles. Telson with median sulcus deep anteriorly, progressively shallower posteriorly, disappearing just before reaching base of lateral spines; terminal portion length 3.3-4.0 times basal width; lateral spines short, 1-1.4 times basal width of terminal portion. Mesial ramus of uropod reaching to, or slightly surpassing, apex of telson; lateral ramus overreaching mesial by as much as 0.2 of its own length, and armed with minute distolateral spine, reaching distal margin of ramus.

Petasma (Figure 54*A, B*) cincinnulate along proximal 0.70 of median line; broad distal part of ventromedian lobule produced into blunt, distomesial projection, its lateral part turned strongly inward; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, border adjacent to ventral costa bearing emargination delimiting basal part from short, broadly subelliptical terminal part; latter inclined toward, and partially covered by, ventromedian lobule, and armed with spinules along entire distal margin; ventral costa with distal part free from, and falling short of, contiguous plate, its distal margin bearing very minute spinules.

Appendix masculina (Figure 54*C, D*) with proximal part broad, produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, directed strongly laterally, and bearing apical tuft of long setae. Appendix interna shorter than appendix masculina, narrow, and lacking setae. Ventrolateral spur large, paddlelike.

Thelycum (Figure 55) with median protuberance on sternite XIV roughly elliptical, low, markedly less elevated than prominent setose, paired convexities of sternite XIII; median ridge of latter long, lacking tooth, sometimes ending in small knob at one or both extremities.

Maximum size.–Female (holotype), 25.5 mm cl, 100 mm tl; male, 18.5 mm cl, 72.5 mm tl (Kubo 1949). Largest male examined by me, 14 mm cl, about 64 mm tl.

Geographic and bathymetric ranges.–Madagascar (off northwest coast) through the Indo-West Pacific to Hawaii (Figure 16), in depths between 180 and 500 m (Figure 9). The few records available are from scattered localities.

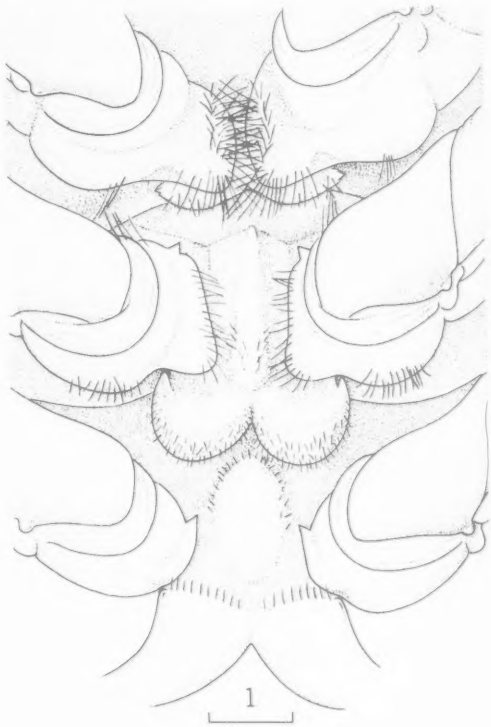

FIGURE 55.—*Hadropenaeus lucasii*, ♀ 19.5 mm cl, Pailolo Channel, Hawaiian Islands. Thelycum, ventral view.

Affinities.–Hadropenaeus lucasii is closely allied to its two Atlantic congeners, *H. affinis* and *H. modestus*, but it may be distinguished from them by the possession of a conspicuous carina on the rostrum dorsal to the adrostral carina, and by certain petasmal and thelycal features. In *H. lucasii* the ventromedian lobule of the petasma is not produced into a distolateral projection; instead, its lateral portion is turned strongly inward; the distal plate of the ventrolateral lobule bears spinules along the entire terminal margin and is produced in a blunt, ventral projection; in addition, the ventral costa falls conspicuously short of the distalmost part of the adjacent plate. The thelycum, in turn, is characterized by a median protuberance on sternite XIV, which does not project ventrally so far as the posterior convexities of sternite XIII, and the latter bears a low median ridge which is not produced anteriorly in a large tooth. Furthermore, in females of *H. lucasii*, the coxae of the fourth pair of pereopods bear a conspicuous anteromesial spine which is lacking in the other two species.

Hadropenaeus lucasii exhibits some morphological variations which are undoubtedly taxonomically insignificant because extremes of variations occur in animals from the same region and even from the same locality. Among them are the relative extension of the scaphocerite, gnathal and thoracic appendages, the total number of rostral teeth as well as the number situated on the carapace. The evidence at hand, however, indicates that the ventral antennular flagellum and some features of the petasma differ regionally. The ventral antennular flagellum is somewhat depressed in the holotype from New Guinea, in Japanese specimens (Kubo 1949) and in two specimens from Madagascar examined by me, and subcylindrical in individuals from Indonesia (de Man 1911) as well as in all those available from Hawaii. In addition, the distomesial projections of the ventromedian lobules of the petasma are larger in specimens from Japan than in males from Madagascar and Hawaii. Whereas the shape of the flagellum exhibits definite variations which seem to be regionally restricted, the differences in the petasma are limited to degree of development and are perhaps insignificant. Except for the collection from Hawaii, available material is extremely meager; consequently, the variations that I have noted are pointed out, with the conviction that definite conclusions as to their taxonomic value must await examination of adequate collections from various areas throughout the Indo-West Pacific.

I have examined the female from the Maldive Islands, Indian Ocean, that Ramadan (1938) identified as *H. lucasii*. This specimen differs from other specimens of the latter species in the following features: the rostral and epigastric teeth are slenderer—not much stronger than the postorbital spine—and inclined more anteriorly; the anteromesial spine on the coxa of the fifth pereopod is longer and more slender; and the median protuberance on sternite XIV is smaller and surrounded by a shallow depression. Crosnier and Forest (1973), who presented an illustration of the thelycum of the specimen (plate 85, figure a), suggested that the slight differences between the thelycum of the latter and that of the type of *H. lucasii* could be due to the difference in size of the animals, the type being 90 mm long (23.5 mm cl) and Ramadan's specimen 70 mm. As these authors indicated, Ramadan's specimen exhibits 6 middorsal teeth (rostral plus epigastric), 3 of which are located on the carapace; this number and arrangement of teeth occurs infrequently in members of *H. lucasii*, but has been observed in several specimens by both Rathbun (1906) and me. Crosnier and Forest suggested further that because of the number and arrangement of the middorsal teeth and the relative size of those behind the rostrum (which are not much stronger than the postorbital spine), Ramadan's specimen might be referable to Borradaile's (1910) *Haliporus malhaensis*. This species was described from Saya de Malha, Indian Ocean, and its identity is still uncertain, primarily because the holotype, the only specimen on which the description was based, is no longer extant (Ramadan 1938). The features pointed out above suggest that the shrimp from the Maldive Islands might belong to a species other than *H. lucasii*, but an understanding of its systematic position must await more material from the Indian Ocean.

Both Burkenroad (1936) and Ramadan (1938) were inclined to think that *H. malhaensis* was identical with *H. lucasii*, and placed the former name in the synonymy of the latter preceded by a question mark. Previously, de Man (1911) had indicated that he would have identified them as one species, except for Borradaile's statement that in *H. malhaensis* neither the fourth nor the fifth pereopod is "particularly slender." De Man also called attention to the fact that in Borradaile's illustration the propodi of the fourth and fifth

pereopods are missing. Kubo (1949) considered that *H. malhaensis* and *H. lucasii* are distinct species; he stated that his specimens of *H. lucasii* cannot be referred to *H. malhaensis* because in the latter there are 3 teeth on the carapace, the scaphocerite does not overreach the antennular peduncle, and the dorsal antennular flagellum is not longer than the ventral which also lacks "rather long setae" on the dorsal and ventral borders. Actually, the first two features are not typical of *H. malhaensis* but occur in *H. lucasii*, in which, as stated above, 3 teeth may be present on the carapace, and the scaphocerite, which usually overreaches the antennular peduncle, extends only to the distal end of the peduncle in some individuals. Features of the antennular flagella of *H. malhaensis* cited by Kubo could be due to the fact that the dorsal flagellum was incomplete in the type, as it often is in preserved specimens, or to omissions of the artist. The two species discussed seem to me to be quite similar, and if there is doubt in my mind as to the status of *H. malhaensis*, it is mainly because of Borradaile's statement that the fourth and fifth pereopods are not "particularly slender." The species exhibits most of the features of *Hadropenaeus:* stout body, thick carapace, short rostrum with ventral margin convex, middorsal teeth on the carapace separated by regularly decreasing intervals, lack of branchiocardiac carina and sulcus, and relative length of the last two pereopods having "fourth leg rather longer and fifth considerably longer than the third." These features of *Hadropenaeus* combined with a fifth pereopod that is not very slender, however, are unique. Perhaps the question of the identity of Borradaile's species will be resolved when large collections of solenocerids from the Indian Ocean are studied. Meanwhile, I am inclined, tentatively, to assign *H. malhaensis* to the synonymy of *H. lucasii*.

Mesopenaeus New Genus

Parartemesia Bouvier 1905b:747 [part, excluding *Parartemesia carinata* Bouvier 1905b = *Pleoticus muelleri* (Bate 1888)].
Haliporus. Bouvier 1906b:1 [part]; 1908:78[part]. A. Milne Edwards and Bouvier 1909:206 [part].
Hymenopenaeus. Burkenroad 1936:102 [part]. Roberts and Pequegnat 1970:29 [part].

Diagnosis.–Body stout, carapace proportionately short; integument thick, firm. Rostrum short, reaching approximately to base of second antennular article; deep, with ventral margin pronouncedly convex, and armed only with dorsal teeth; epigastric tooth and first rostral separated by interval similar to that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian and branchiostegal spines absent. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac carina and sulcus, posthepatic, and submarginal carinae lacking. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long, flexible. Antennular flagella not much longer than carapace and dissimilar: dorsal flagellum subcylindrical and slender, ventral one conspicuously depressed. Mandibular palp two jointed, articles broad, distal one almost as long as basal and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fourth and fifth pereopods rather stout proximally, fifth moderately longer than fourth. First pereopod with spine on basis and ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal). In males, petasma with ventral costa not projecting free distally, there bearing flexible flap; distal portion of rib of dorsolateral lobule projecting beyond margin of adjacent area; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into long ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia on somites IX to XIV; single, rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII; podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

Type-species.–*Parartemesia tropicalis* Bouvier 1905b.

Etymology.–The generic name is derived from the Greek mesos, something in between, in combination with the generic name *Penaeus*, alluding to the fact that the dorsal antennular flagellum is subcylindrical and filiform, as in *Pleoticus*, *Haliporoides* and *Hymenopenaeus*, and the ventral one flattened, much as in *Solenocera*.

Gender.–Masculine.

List of species.–This genus includes only one species: the western Atlantic *Mesopenaeus tropicalis* (Bouvier 1905b).

Affinities.–Mesopenaeus resembles *Solenocera* in possessing a flattened ventral flagellum, but in the former this appendage is neither so flattened and broad nor is it channeled as it is in the latter. It shares with its more closely allied genera—*Hymenopenaeus, Haliporoides, Pleoticus,* and *Hadropenaeus*—a subcylindrical dorsal flagellum, and a similar armature of the lateral ramus of the uropod, the lateral rib of which ends in a well-defined spine. The stout body, deep rostrum with the ventral margin pronouncedly convex, arrangement of the epigastric and rostral teeth, and absence of both branchiocardiac sulcus and carina place *Mesopenaeus* closer to *Hadropenaeus* than to the other genera. *Mesopenaeus* differs from *Hadropenaeus,* however, in that the ventral flagellum is invariably depressed, whereas in the latter it is almost always subcylindrical (in occasional individuals of *H. lucasii* the ventral flagellum is depressed). In *Mesopenaeus* orbital and branchiostegal spines are present, and the thelycum exhibits paired anterior protuberances on sternite XIV which are present elsewhere among the solenocerids only in the members of the nominal genus. Finally, in *Mesopenaeus* the ventral costa of the petasma is fused to the flexible terminal part of the ventrolateral lobule, whereas in *Hadropenaeus* the ventral costa is distally free from the sclerotized terminal part of the lobule.

Mesopenaeus tropicalis (Bouvier 1905)

Figures 9, 34, 56-63

Parartemesia tropicalis Bouvier 1905b:748 "mer des Antilles" in 80-175 fm (146-329 m). [No type designated.]

Haliporus tropicalis. Bouvier 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909:217, fig. 45-54, pl. 3, fig. 1-19 [lectotype ♀, MCZ 7199; type-locality: "Blake: Florida Bank, lat. N. 26° 31′, long. 0. 85° 03′, 119 brasses." Paralectotype ♀, MP, off Barbados, 13°04′12″N, 59°36′45″W, 76 fm (139 m), 5 March 1879, *Blake* stn 272]. de Man 1911:7.

Hymenopenaeus tropicalis. Burkenroad 1936:103. Springer and Bullis 1956:8. Boschi 1964:38. Bullis and Thompson 1965:5. Williams 1965:15, fig. 5-7. Cerame-Vivas and Gray 1966:263. Mistakidis and Neiva 1966:434. Roberts and Pequegnat 1970:29. Pequegnat and Roberts 1971:8. Iwai 1973:44, fig. 13.

Solenocera weymouthi Lindner and Anderson 1941:181, fig. 1a-e [holotype ♀, USNM 79357; type-locality: off Orange Beach, Ala., 29°28′N, 87°30′W, 46 fm (84 m), *Pelican* stn 137-2, 1 March 1939; allotype ♂, USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, *Anton Dohrn* stn 74-32; paratype ♂, USNM 79358, locality as in holotype; 71 ♂ 78 ♀, USNM 23420, between Cape Hatteras and Cape Lookout, N.C., 34°35′30″N, 75°45′30″W, 32 fm (59 m), 18 October 1885, *Albatross* stn 2605]. Anderson and Lindner 1945:286.

Hypenepenaeus tropicalis. Mistakidis 1965:9.

Material

UNITED STATES—North Carolina: 2 ♂ 1 ♀, UNC-IMS, NE of Cape Lookout, 90-110 m, 27 April 1965, *Eastward* stn 1087. 71 ♂ 78 ♀ (paratypes *Solenocera weymouthi*), USNM 23420, NE of Cape Lookout, 59 m, 18 October 1885, *Albatross* stn 2605. 1 ♀, USNM, SE of Cape Lookout, 82 m, 21 June 1957, *Combat* stn 406. 1 ♂ 1 ♀, UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, *Albatross III* stn 21-4. 8 ♂ 8 ♀, USNM, SE of Cape Lookout, 154 m, 8 June 1949, *Albatross III.* 2 ♂ 4 ♀, UNC-IMS, E of Cape Fear, 100 m, 27 April 1965, *Eastward* stn 1089. 1 ♂, UNC-IMS, SE of Cape Fear, 140-145 m, 27 April 1965, *Eastward* stn 1086. 2 ♂ 2 ♀, USNM, SE of Cape Fear, 183 m, 29 January 1972, *Oregon II* stn 11747. 3 ♂ 5 ♀, USNM, off Cape Fear, 190-187 m, 29 February 1960, *Silver Bay* stn 1694. 1 ♂ 8 ♀, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, *Silver Bay* stn 1693. South Carolina: 1 ♀, USNM, off Cape I, 183 m, 28 January 1972, *Oregon II* stn 11743. 1 ♀, USNM, E of Bull Bay, 181 m, 5 January 1885, *Albatross* stn 2313. 2 ♀, USNM, E of Bull Bay, 155 m, 5 December 1960, *Silver Bay* stn 2535. 1 ♀, USNM, off Santa Helena Sound, 83 m, 28 April 1966, *Oregon* stn 6073. Georgia: 4 ♀, USNM, off Savannah, 68-91 m, 14 December 1961, *Silver Bay* stn 3658. 7 ♂ 2 ♀, USNM, off Savannah, 73 m, 12 March 1956, *Bowers* stn 54. 1 ♀, USNM, off Savannah Beach, 73 m, 26 April 1966, *Oregon* stn 6062. 1 ♂, USNM, off Catherines Sound, 37 m, 13 March 1940, *Pelican* stn 195-10. Florida: 1 ♀, USNM, off Fernandina, 179 m, 18 January 1972, *Oregon II* stn 11699. 1 ♂ 9 ♀, USNM, off St Augustine, 75 m, 24 April 1966, *Oregon* stn 6044. 1 ♂ 3 ♀, USNM, off St Augustine, 40 m, 5 September 1962, *Silver Bay* stn 4340. 1 ♀, USNM, off Matanzas Inlet, 183 m, 18 November 1965, *Oregon* stn 5741. 1 ♀, USNM, off Matanzas Inlet, 64-87 m, 7 October 1962, *Silver Bay* stn 4451. 1 ♀, USNM, off Ponce de Leon Inlet, 73-97 m, 5 October 1962, *Silver Bay* stn 4420. 1 ♂ 1 ♀, USNM, off Edgewater, 51-37 m, 24 August 1965, *Oregon* stn 5603. 1 ♀, USNM, off Cape Kennedy, 70 m, 16 January 1966, *Oregon* stn 5860. 1 ♀, USNM, off Melbourne Beach, 73 m, 14 July 1961, *Silver Bay* stn 3279. 1 ♀, UMML, NE of St Lucie Inlet, 38-42 m, 21 May 1968, *Gerda* stn 1002. 1 ♂, UMML, SE of St Lucie Inlet, 60-62 m, 21 May 1968, *Gerda* stn 1001. 1 ♀, RMNH, E of Miami, 119 m,

16 April 1965, *Gerda* stn 622. 3 ♀, RMNH, off Elliott Key, 82-77 m, 15 April 1965, *Gerda* stn 610. 2 ♀, USNM, off Old Rhodes Key, 91 m, 10 November 1961, *Silver Bay* stn 3524. 2 ♂ 3 ♀, USNM, off Key Largo, 86-79 m, 10 July 1967, *Gerda* stn 834. 1 ♂ 2 ♀, RMNH, off Key Largo, 86-95 m, 14 September 1965, *Gerda* stn 752. 1 ♂ 2 ♀, RMNH, off Key Largo, 92-97 m, 14 September 1965, *Gerda* stn 751. 1 ♀, UMML, off Key Largo, 108-88 m, 26 January 1966, *Gerda* stn 767. 2 ♀, RMNH, off Key Largo, 146 m, 26 January 1966, *Gerda* stn 770 . 1 ♀, USNM + 4 ♂ 2 ♀, RMNH, off Key Largo, 99-91 m, 10 July 1967, *Gerda* stn 833. 4 ♂ 2 ♀, RMNH, SE of Key Largo, 95 m, 15 April 1965, *Gerda* stn 602. 1 ♂ 1 ♀, USNM, off Key Largo, 102 m, 9 April 1886, *Albatross* stn 2639. 1 ♀, USNM, Hawk Channel, 110 m, 27 October 1960, *Silver Bay* stn 2391. 1 ♂ 9 ♀, USNM, Hawk Channel, 128 m, 27 October 1960, *Silver Bay* stn 2392. 1 ♂ 1 ♀, USNM, SE of Key West, 93-106 m, 25 February 1969, *Gerda* stn 1024. 2 ♂ 2 ♀, USNM, SE of Key West, 135-146 m, 25 February 1969, *Gerda* stn 1028. 2 ♂, USNM, off Key West, 179 m, 14 February 1902, *Fish Hawk* stn 7279. 1 ♂, USNM, SW of Marquesas Keys, 196-210 m, 26 April 1969, *Gerda* stn 1084. 1 ♂, USNM, SW of Marquesas Keys, 201-210 m, 26 April 1969, *Gerda* stn 1085. 2 ♀, USNM, SW of Marquesas Keys, (depth not given), 12 December 1962, *Oregon* stn 4142. 2 ♂ 2 ♀, USNM, S of Dry Tortugas, 366 m, 10 July 1965, *Oregon* stn 1330. 1 ♂, USNM, S of Dry Tortugas, 229-274 m, 28 April 1969, *Gerda* stn 1095. ♂ (allotype *S. weymouthi*), USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, *Anton Dohrn* stn 74-32. 1 ♂, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 1 ♀, USNM, SW of Dry Tortugas, 183 m, 6 August 1963, *Oregon* stn 4370. 1 ♂ 21 ♀, USNM, NW of Dry Tortugas, 298 m, 19 April 1954, *Oregon* stn 1026. ♀ lectotype, MCZ 7199, Florida Bank, 218 m, *Blake*. 4 ♂ 1 ♀, USNM, off St Petersburg, 106 m, 18 March 1954, *Oregon* stn 938. 2 ♀, USNM, W of Clearwater, 146 m, 11 March 1956, *Oregon* stn 920. 6 ♂ 12 ♀, USNM, off Apalachicola Bay, 88 m, 10 March 1954, *Oregon* stn 917. 2 ♂ 7 ♀, USNM, S of St Vincent I, 64 m, 7 March 1954, *Oregon* stn 896. 1 ♂, USNM, off Panama City, 101-130 m, 26 July 1957, *Silver Bay* stn 100. 4 ♂ 3 ♀, USNM, off Choctawhatchee Bay, 91 m, 21 March 1954, *Oregon* stn 944. 2 ♀, USNM, off Gulf Beach, 165 m, 1 March 1955, *Oregon* stn 1254. Alabama: ♀ (holotype *S. weymouthi*), USNM 79357, off Orange Beach, 84 m, 1 March 1939, *Pelican* stn 137-2. 1 ♂ (paratype *S. weymouthi*), USNM 79358, same locality as holotype.

MEXICO—Quintana Roo: 2 ♂ 18 ♀, USNM, NE of Cape Catoche, 183 m, 22 January 1967, *Oregon* stn 6399.

BAHAMA ISLANDS—1 ♂ 3 ♀, USNM, NE of Little Bahama Bank, 183 m, 25 October 1961, *Silver Bay* stn 3466. 1 ♀, RMNH, Northwest Providence Channel, 278-329 m, 3 March 1965, *Gerda* stn 526. 1 ♂ 4 ♀, RMNH, off Great Isaac I, 311-329 m, 2 March 1965, *Gerda* stn 509. 1 ♂, USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, *Gerda* stn 815. 1 ♀, USNM, off Great Inagua, 183-137 m, 5 November 1961, *Silver Bay* stn 3502. 1 ♂ 1 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10849. 1 ♂ 4 ♀, USNM, S of Great Inagua, 311 m, 13 December 1969, *Oregon II* stn 10850.

CUBA—2 ♂, USNM, N of Las Villas, 461 m, 15 December 1969, *Oregon II* stn 10860.

DOMINICAN REPUBLIC—1 ♂ 1 ♀, USNM, off Cabo Engaño, 201 m, 17 October 1963, *Silver Bay* stn 5188.

PUERTO RICO—2 ♂ 2 ♀, USNM, Mona Passage, 366 m, 17 October 1963, *Silver Bay* stn 5190.

LESSER ANTILLES—2 ♀, USNM, Dominica Passage, 640 m, 1 December 1969, *Oregon II* stn 10825. 1 ♀, USNM, off Barbados, 91-366 m, J. B. Lewis. 1 ♀ paralectotype, MP, off Barbados, 139 m, 5 March 1878, *Blake* stn 272.

WESTERN CARIBBEAN—18 ♂ 12 ♀, USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, *Gerda* stn 954. 1 ♂ 5 ♀, USNM, Arrowsmith Bank, 252-293 m, 14 March 1968, *Pillsbury* stn 591. 1 ♂ 2 ♀, USNM, Arrowsmith Bank, (depth not given), 15 November 1968, *Pillsbury* stn 598. 1 ♂, UMML, Arrowsmith Bank, 115-190 m, 23 August 1970, *Gerda* stn 1286. 1 ♂ 1 ♀, USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, *Gerda* stn 951. 1 ♂, USNM, Arrowsmith Bank, 225-437 m, 21 August 1970, *Gerda* stn 1275. 1 ♀, USNM, NE of Banco Gorda, 265-274 m, 6 June 1962, *Oregon* stn 3622. 2 ♀, UMML, NW of Quita Sueño Bank, 296-375 m, 31 January 1971, *Pillsbury* stn 1356. 1 ♂ 1 ♀, USNM, W of Quita Sueño Bank, 201-207 m, 12 February 1967, *Oregon* stn 6460. 22 ♂ 24 ♀, USNM, W of Isla de Providencia, 289-274 m, 4 February 1967, *Oregon* stn 6423. 1 ♂ 5 ♀, USNM, SW of Isla de San Andrés, 201-219 m, 4 February 1967, *Oregon* stn 6424. 18 ♂ 20 ♀, USNM, W of Isla de San Andrés, 139 m, 6 February 1967, *Oregon* stn 6434. 6 ♂ 10 ♀, USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, *Oregon* stn 6444.

BELIZE—1 ♂ 3 ♀, USNM, W of Lighthouse Reef, 329-274 m, 24 January 1966, *Oregon* stn 6404. 1 ♀, USNM, W of Lighthouse Reef, 262 m, 23 January 1967, *Oregon* stn 6403. 6 ♂ 7 ♀, USNM, W of Lighthouse Reef, 183 m, 24 January 1967, *Oregon* stn 6405.

NICARAGUA—1 ♀, USNM, NE of Puerto Cabezas, 183-219 m, 21 May 1962, *Oregon* stn 3568. 1 ♀, USNM, NE of Puerto Cabezas, 274-293 m, 21 May 1962, *Oregon* stn 3566. 11 ♂ 23 ♀, USNM, 190 m, off La Barra de Río Grande, 5 February 1967, *Oregon* stn 6426. 7 ♂ 3 ♀, USNM, off La Barra de Río Grande, 176-110 m, 5 February 1967, *Oregon* stn 6427. 18 ♂ 10 ♀, USNM, NE of Islas del Maíz, 119 m, 5 February 1967, *Oregon* stn 6432. 23 ♂ 18 ♀, USNM, NE of Islas del Maíz, 192-198 m, 7 February 1967, *Oregon* stn 6448. 5 ♀, USNM, NE of Islas del Maíz, 198-201 m, 7 February 1967, *Oregon* stn 6447.

PANAMA—1 ♂, USNM, off Coclé del Norte, 137 m, 29 May 1962, *Oregon* stn 3587.

VENEZUELA—2 ♂ 1 ♀, USNM, off Golfo de Venezuela, 201 m, 26 September 1963, *Oregon* stn 4398. 1 ♀, USNM, off Puerto Cumarebo, 161-187 m, 27 July 1968, *Pillsbury* stn 757. 2 ♂ 3 ♀, USNM, E of Pen de Paraguaná, 915 m, 4 October 1963, *Oregon* stn 4416. 1 ♂, USNM, off La Guaira, 97 m, 13 October 1963, *Oregon* stn 4459. 1 ♂ 1 ♀, USNM, off La Guaira, 97 m, 13 October 1963, *Oregon* stn 4461. 2 ♂, UMML, W of I La Tortuga, 68-60 m, 22 July 1968, *Pillsbury* stn 734. 26 ♂ 11 ♀, USNM, off Cabo Cordera, 60-73 m, 22 July 1968, *Pillsbury* stn 737. 6 ♂ 3 ♀, USNM, NE of Islas Los Testigos, 585-439 m, 24 September 1964, *Oregon* stn 5039. 2 ♀, USNM, NE of Islas Los Testigos, 128-119 m, 24 September 1964, *Oregon* stn 5040.

BRAZIL—Amapá: 1 ♂ 1 ♀, USNM, mouths of the Amazon River, 229 m, 17 November 1957, *Oregon* stn 2080. Maranhão: 1 ♀, USNM, off São Luis, 183 m, 9 March 1963, *Oregon* stn 4225. São Paulo: 1 ♂ 1 ♀, IOUSP, SSE of I de São Sebastião, 156-152 m, 3 July 1971, *Prof. W. Besnard* stn 1471. 4 ♂ 2 ♀, USNM-MP, SE of Quemado Grande I, 97-100 m, 11 December 1961, *Calypso* stn 138.

Description.–Body robust (Figure 56), integument firm, mostly glabrous, but carapace with rather long densely set setae on rostrum above adrostral carina; patch of minute setae extending from orbital margin to base of epigastric tooth; and elongate patch of sparsely set setae below hepatic sulcus.

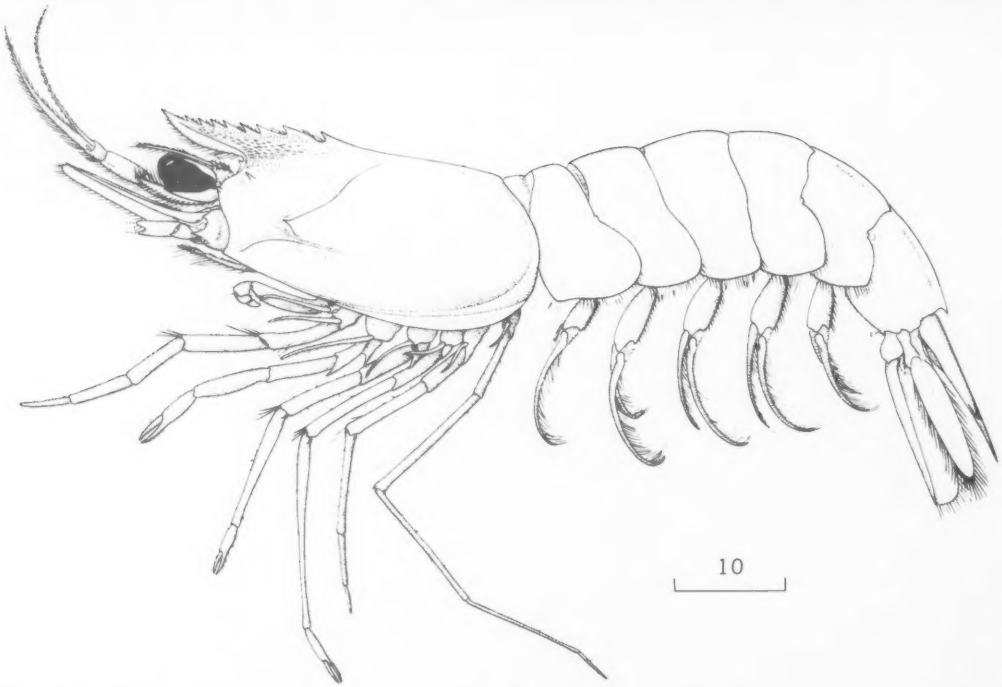

FIGURE 56.—*Mesopenaeus tropicalis*, ♀ 23.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Lateral view.

Rostrum rather short, its length not exceeding 0.4 that of carapace, reaching, at most, base of second antennular article, straight or slightly tilted upward, moderately high, its ventral margin strongly convex, often with subapical concavity giving rise to saber shaped tip. Rostral plus epigastric teeth 7-10, mode 8 (percentage distribution in North America: 7-2, 8-60, 9-36, 10-2, N = 100; percentage distribution in South America: 7-4, 8-80, 9-15, 10-1, N = 100); teeth long and sharp; usually third rostral tooth, sometimes second, at level of orbital margin. Adrostral carina sharp, extending from orbital margin to ultimate tooth; postrostral carina low, short, extending only to level of cervical sulcus. Orbital spine with broad base, short but sharp; postorbital spine longest of lateral spines on carapace; antennal spine moderately long, and hepatic spine about same length. Cervical sulcus deep, gently sinuous, extending almost to, but not crossing, postrostral carina, ending at about 0.55 cl; hepatic sulcus almost horizontal posteriorly, turning anteroventrally in broad arc below hepatic spine, and nearly reaching anterior margin of carapace.

Eye (Figure 57) with basal article produced distomesially into densely pubescent, elongate, narrow scale; ocular peduncle short; cornea rather broad, greatest diameter about 1.8 times that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Mandibular palp (Figure 58*A*) broad, distal article almost as long as proximal, and armed with unique distomesial series of hooks. First maxilliped as illustrated (Figure 58*B*); rudimentary arthrobranchia on articular membrane (Figure 58*Bc-c*^{1}). Antennular peduncle length about 0.6 cl; prosartema long, reaching as far as midlength of second antennular article; stylocerite long, spiculiform distally, its length about 0.7 of distance between its base and that of distolateral spine; latter rather long, very slender, and sharp. Ventral antennular flagellum typically depressed, slightly shorter than subcylindrical dorsal flagellum. Flagella longer in North American than in West Indian, Central American, and South American populations (Figure 59). Ratio of

length of dorsal flagellum to length of carapace in North American shrimp ranging from about 1.15 in 10-mm cl individuals to about 0.95 in 23-mm cl shrimp. In Bahamian and southern populations, ratio decreasing from about 0.95 in shrimp 10 mm cl to about 0.6 in shrimp 24 mm cl. Scaphocerite not reaching distal margin of antennular peduncle or exceeding it by as much as 0.1 of its own length; lateral rib ending distally in long spine, usually extending to level of distal margin of lamella; antennal flagellum at least 3.5 times total length of shrimp: 110-mm tl female with flagellum 385 mm long (measurements taken by me of specimen caught south of Great Inagua, Bahama Islands, in 311 m, at *Oregon II* stn 10849). Third maxilliped usually exceeding antennular peduncle by length of dactyl, occasionally surpassing it by length of dactyl and as much as 0.2 that of propodus; length of dactyl about 0.75 that of propodus.

First pereopod, stoutest of five, reaching at most distal end of carpocerite. Second pereopod surpassing carpocerite by length of dactyl or by entire length of propodus. Third pereopod exceeding antennular peduncle by 0.6 to entire length of propodus. Fourth pereopod overreaching carpocerite by 0.5 or more length of dactyl. Fifth pereopod, longest of five, exceeding antennular peduncle by length of dactyl or by latter and as much as 0.2 length of propodus. Order of pereopods in terms of their maximal anterior extensions: first and fourth, second, third and fifth. First pereopod with long, strongly pointed spines on basis and ischium; second pereopod with long sharp spine on basis. In female, coxa of third pereopod produced into plate extending mesially, then uniquely folded ventrolaterally; coxa of fourth pereopod produced in strong plate resembling head of bird, "beak" consisting of long, sharp spiniform projection directed posteriorly, entire plate curving around lateral horn on plate of sternite XIII; coxa of fifth pereopod bearing short plate produced anteromesially in blunt projection. In male, coxa of fourth pereopod with short plate bearing small anterior tooth; fifth pereopod with large subtriangular tooth on anterior margin.

FIGURE 57.—*Mesopenaeus tropicalis*, ♀ 25 mm cl, off Key Largo, Fla. Eye.

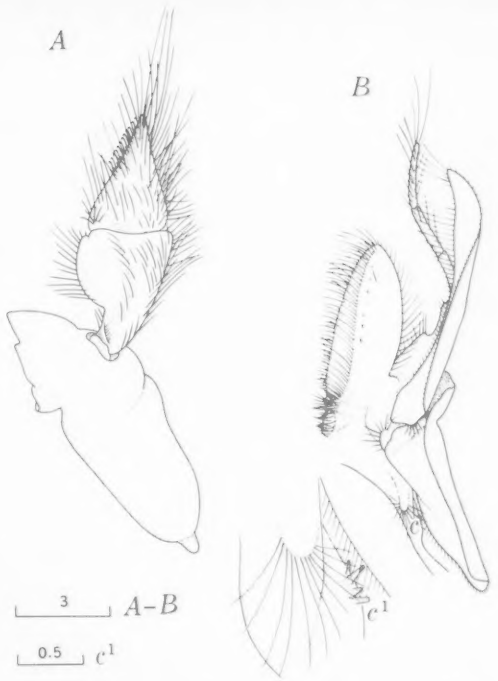

FIGURE 58.—*Mesopenaeus tropicalis*, ♀ 20 mm cl, west of Light House Reef, Belize. *A*, Mandible. *B*, First maxilliped. *c*, Arthrobranchia. c^1, Enlargement of *c* (all from left side).

Abdomen with sharp, high, middorsal carina from third to sixth somites; low, rounded, sometimes barely perceptible carina on second somite in larger specimens; posterodorsal margin of third through fifth somites with median incision; sixth somite with small, sharp spine at posterior end of carina, and pair of small spines posteroventrally. Telson with median sulcus deep anteriorly and penetrated posteriorly by longitud-

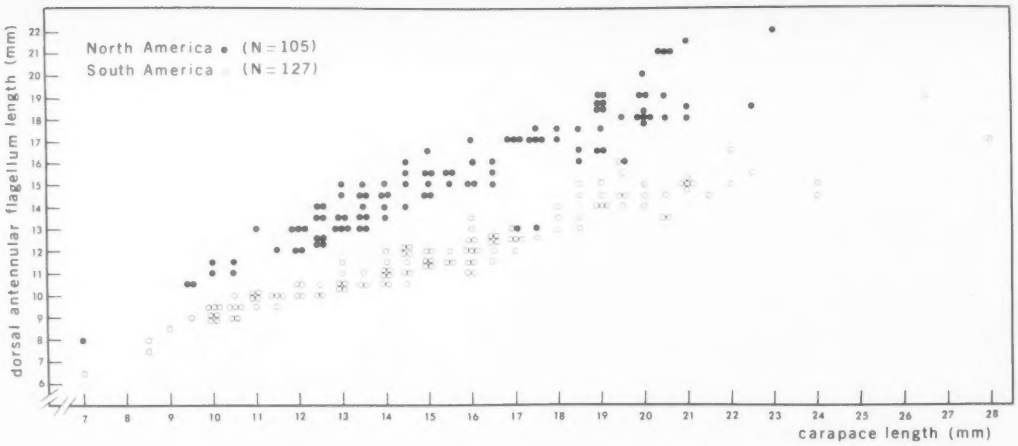

FIGURE 59.—*Mesopenaeus tropicalis*. Relationship between length of dorsal antennular flagellum and carapace length.

inal elevation merging with convex terminal portion; latter moderately long, its length 4-5 times basal width; lateral spines short, 0.9-1.4 times basal width of terminal portion; mesial ramus of uropod reaching tip of telson or overreaching it by no more than 0.1 of its own length; lateral ramus surpassing mesial ramus by 0.1-0.2 of its own length, and bearing small, terminal, distolateral spine.

Petasma (Figure 60*A, B*) cincinnulate along proximal 0.7 of median line and with terminal margin lacking spinules, often minutely rugose across ventromedian lobule; distal portion of ventromedian lobule thick, flexible, folded, its mesial portion strongly excavate ventrally, and overlying its shorter lateral portion; latter produced laterally into process resembling bird head in silhouette, dorsolateral lobule with heavy rib curved in hooklike terminal portion lying against ventral surface of process; inner surface of dorsolateral lobule studded with minute setae mesially and bearing proximolateral row of long setae; corresponding, but shorter, row of long setae on outer surface. Ventral costa reaching distally as far as, or slightly overreaching, row of cincinnuli, trending dorsally, and bearing flexible subrectangular, marginal flap, extending horizontally almost perpendicular to costa.

Appendix masculina (Figure 60*C, D*) very elongate, convex dorsally, deeply channeled ventrally, its proximal part produced laterally into rounded, ventrally turned lobe; distal part tapering, its tip twisted mesiad, mesial surface deeply concave, and armed with densely set, relatively long setae on proximolateral border, short setae on borders of concavity, and tuft of long setae apically. Appendix interna almost as long as appendix masculina, broad, subelliptical, bearing lateral rib, abutting corresponding border of appendix masculina, and armed with tuft of long setae on distolateral border, and very short setae on mesial border. Basal sclerite obliquely crossed by heavy ridge separating deep proximal concavity from anterior depressed area, and with its ventrolateral spur proximally rounded and strongly attenuate distally.

Thelycum (Figure 61) with paired short, blunt, cushionlike protuberances on flexible anterior part of sternite XIV, contiguous to ventrally raised, heavily sclerotized posterior shield; free border of shield sharp or thickened, and varying from slightly concave to produced into anteromedian, minute spine. Median plate of sternite XIII divided by median longitudinal incision into paired rounded to subrectangular lobes overhanging sternite XIV, each bearing blunt horn anterolaterally. Sternite XII with paired blunt, distally flattened projections overhanging sternite XIII.

Photophores.–Observations by me on freshly collected specimens demonstrated that this species, like *H. affinis* and *H. debilis*, bears photophores, which are arranged as follows: one adjacent to the base of the podobranchia of both the third maxilliped and fourth pereopod, and a pair on the anterior part of the sternum from the second through

the sixth abdominal somites, immediately posterior to the transverse ridge of the preceding segment. The seven pairs of photophores consist of a yellow conical portion and a red lens.

Color.–Body translucent salmon with obliquely vertical, deep yellow stripes, and milky white patches of various sizes on carapace. Rostrum yellow from second rostral tooth to apex, epigastric and first rostral teeth salmon. Carapace with three anterior stripes resembling chevron: anteriormost short, arched, extending from near base of orbital spine posterodorsally to below first rostral tooth; second extending almost from base of postorbital spine to posterior base of epigastric tooth; third posteriorly flanking cervical sulcus, and broadening on middorsum, forming diamond-shaped mark. Additional posterior stripe on carapace narrow on middorsum, broadening rapidly anteroventrally, and then narrowing again, forming band along dorsal part of branchiostegite. White patches on carapace very conspicuous: anterior one subcircular, situated on depression below hepatic spine; second oblong, lying ventral to hepatic sulcus; posteriormost ovate and large, almost covering entire branchiostegite. First abdominal somite with yellow spot immediately anterior to posterolateral hinge, remaining five somites with broad, uniformly wide yellow stripe extending from anterior half of middorsum posteroventrally to lateral hinge, except stripe on sixth reaching posteroventral extremity of pleuron; sixth somite also with short posterodorsal yellow stripe extending from dorsum to lateral base of telson; midventral part of pleura of anterior five somites with deep salmon spot, sixth somite with deep salmon patch on anteroventral part of pleuron. Telson salmon, with median sulcus yellow; uropodal rami bearing broad transverse band across midlength. Antennulae and antennae deep salmon, darker on basicerite of antenna and on adjacent anteroventral portion of carapace. Thoracic sternites, first and second maxillipeds, and proximal podomeres (including merus) of third maxilliped and pereopods pale salmon; distal podomeres deep salmon except for narrow milky white longitudinal band. Basis of pleopods deep salmon preaxially with lateral part milky white; endopods and exopods whitish with orange line along midlength; ventral surface of

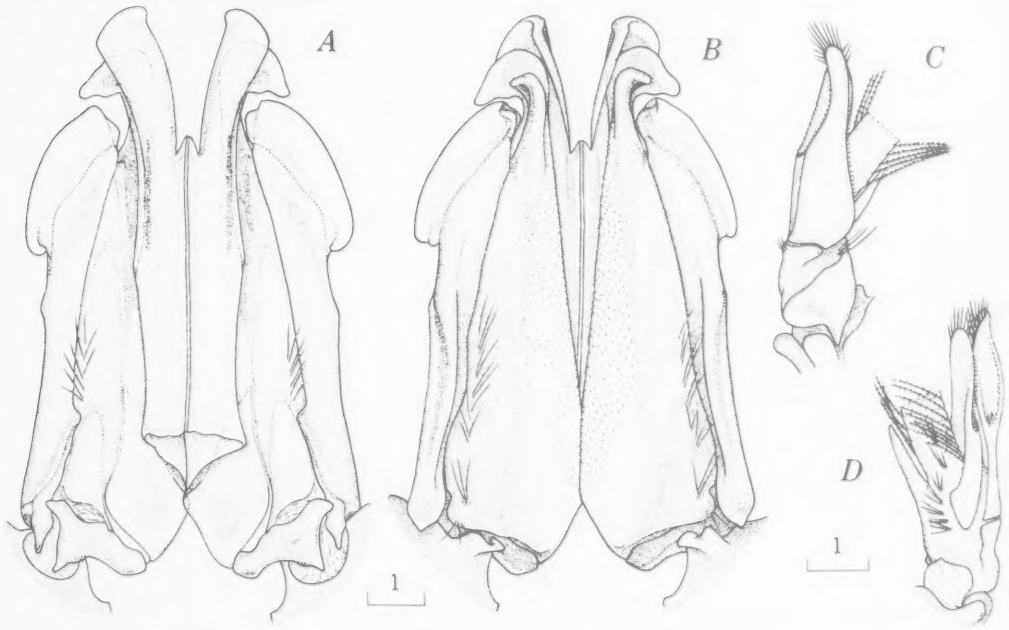

FIGURE 60.—*Mesopenaeus tropicalis*, ♀ 17.5 mm cl, east of Cayos de Albuquerque, western Caribbean. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendices masculina and interna, dorsal view. *D*, Ventromesial view.

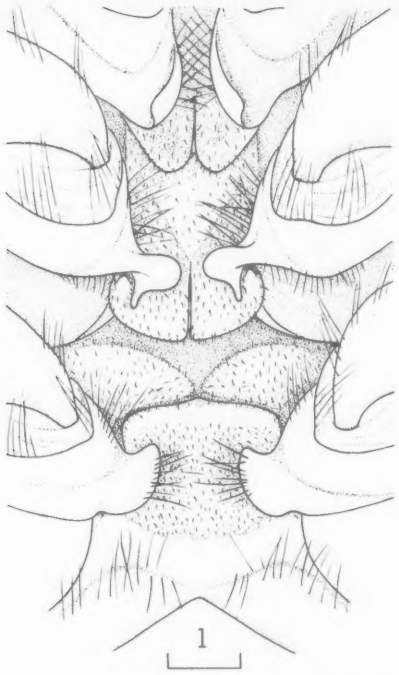

FIGURE 61.—*Mesopenaeus tropicalis*, ♀ 25.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Thelycum, ventral view.

abdomen with orange transverse rib at posterior margin of sternites, interrupting overall translucent salmon.

Although the color pattern described is altered with the expansion and contraction of the chromatophores, this basic arrangement of colors was usually recognizable in all specimens examined by me. However, according to Iwai (1973), this species exhibits an overall red in Brazilian waters.

Maximum size.–Males: 20.5 mm cl; females: 28 mm cl.

Geographic and bathymetric ranges.–Northeast of Cape Lookout, N.C. (34°43′N, 76°40′W), to the Straits of Florida, and into the Gulf of Mexico to Alabama. Also off the Bahamas, through the Caribbean, and along the Atlantic coast of South America as far as Rio Grande do Sul (Figure 34). The record from Rio Grande do Sul (34°00′S) is from Iwai (1973). This species occurs at depths between 30 and 915 m (Figure 9), thus from relatively shallow waters (where it is infrequent) on the continental shelf to the upper zone of the continental slope. This bathymetric range is not peculiar to *M. tropicalis*, but is also exhibited by various other penaeoids. The single record of the shrimp from northeast of Cape Catoche, and its apparent absence in the Gulf of Mexico from Mississippi to northern Yucatán, suggest inadequate sampling in the region. Its presence on the continental slope, even if only in the shallower zone, where no barriers prevent its dispersion, also favors this conclusion.

According to the limited data at my disposal, in the warm temperate waters of North America this species tends to remain on the continental shelf, where 85% of the samples examined by me were caught; in contrast, off the Bahamas and to the south, it seems to be more abundant off the shelf edge, where 76% of the samples were taken. In neither region do the animals appear to exhibit a seasonal migration, moving from warmer waters of the shelf to greater depth in late fall and returning in the spring.

Affinities.–Mesopenaeus tropicalis, ths sole member of the genus, differs strikingly from the other solenocerids occurring in the western Atlantic in possessing antennular flagella which are dissimilar in shape, the dorsal one subcylindrical and the ventral depressed.

Variations in the relative length of the antennular flagella were pointed out by Lindner and Anderson (1941). I have confirmed their observations and, in addition, have found that the range of variations in North American populations is different from that in populations occurring from the Bahamas to Brazil, the former having longer flagella than the latter. Noteworthy is the parallelism that exists in the relative length of the antennular flagella between *Mesopenaeus tropicalis* and two closely related allopatric species of the genus *Solenocera*. Like the northern population of *M. tropicalis*, *S. vioscai*, a North American species, possesses longer flagella than does *S. acuminata*, which occurs from the Bahamas to Brazil (Pérez Farfante and Bullis 1973). A similar tendency was observed by Pérez Farfante and Bullis in *S. atlantidis*, the northern populations of which tend to have longer flagella than do those from the Bahamas southward. The thelycum of *M. tropicalis* also exhibits considerable variation, even within a single population, the shield of sternite XIV varying from flat with the anterior

margin bladelike, to deeply excavated on the median portion, and with the anterior margin elevated in a strong ridge; in addition, this margin ranges from bearing a minute anteromedian spine to being concave. Furthermore, the anterolateral protuberances of sternite XIII may be low or rather strongly raised.

Spermatophore.–Compound spermatophore consisting of slender, laterally compressed geminate body continuous with broad anterior lobes, bearing lateral wings, and produced posterolaterally in relatively narrow flanges (Figure 62).

Thick opaque ventral wall and lateral wall of each spermatophore (Figure 63*A*) extending anteriorly forming ventral portion of anterior lobe; lateral wall, opaque anteriorly, translucent posteriorly, bearing fleshy wing; dorsomesial wall (Figure 63*B*) mostly translucent but thickened mesially, continuous with dorsomesial portion of anterior lobe, and extending posteromesially beyond fundus of sac, there joining flange, and giving rise to pocketlike caudal projection. Anterior lobe forming obliquely truncate collar opening laterally and through posterior slit, with ventrolateral surface subrectangular, and dorsomesial surface elongate trapezoidal, broadest laterally. Wing flexible (lacking heavily sclerotized supporting structures), bearing rounded lobe anteriorly. Flange extending from about midlength of sac around posterolateral margin, bearing anteriorly cornified, reniform projection, and produced laterally in roughly semicircular flap. Spermatophore supported by strong C-shaped armature, its mesial part fused to dorsomesial wall and its anterior arm extending across and supporting ventral wall, with lateral extremity forked: anterior branch forming foliaceous process, directed dorsally, facing posterior slit of anterior lobe; posterior branch spirally twisted and located just cephalic to reniform projection of flange. Dorsal plate elongate ovate, extending from base of wing to posterior margin of flange.

Compound spermatophore attached to female with anterior lobes on sternite XII, their elongate lateral openings lying close to gonopores; angles formed by anterior lobes and wings embracing posterior corners of coxal plates of third pereopods; wings extending laterally, attached to sternite XIII, pressing against marginal ridge of XII. Posterior part of geminate body affixed by dorsal plates to shieldlike posterior plate of sternite XIV, elevated (ventrally) well above level of anterior lobes, thus geminate body directed anterodorsally. Posterior parts of flanges sloping posterodorsally, lateral parts attached to sternite XIV, and reniform projections lying near coxae of fourth pereopods. Finally, foliaceous processes meeting on middorsal line, whereas spirally turned branches of C-shaped armature (diverging from bases of foliaceous processes) projecting laterally.

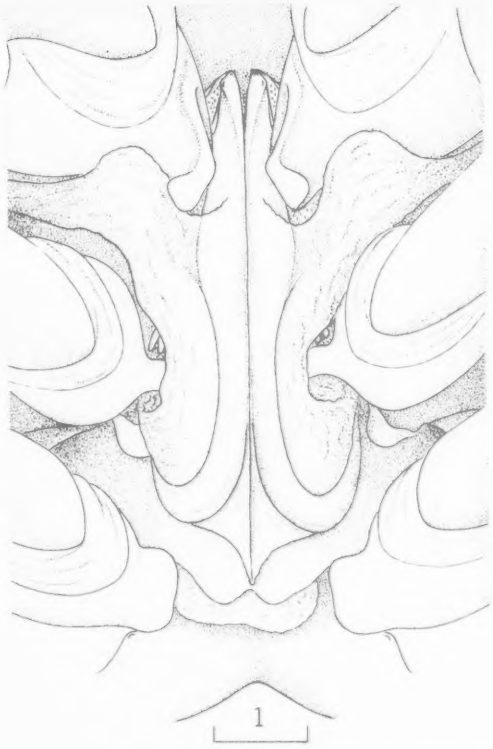

FIGURE 62.—*Mesopenaeus tropicalis*. Compound spermatophore attached to female, ♀ 19.5 mm cl, off Gulf Beach, Fla. (setae omitted).

I have observed sperm masses protruding from the sperm sacs into the cavity of the respective anterior lobe, from which the sperm must be dispersed into the surrounding water adjacent to the female gonopores. A complete compound spermatophore detached by me from an impregnated female was found to lack sperm masses, suggesting that the sperm had been freed while the intact spermatophore was still anchored to the animal; furthermore, there was no trace of such masses on

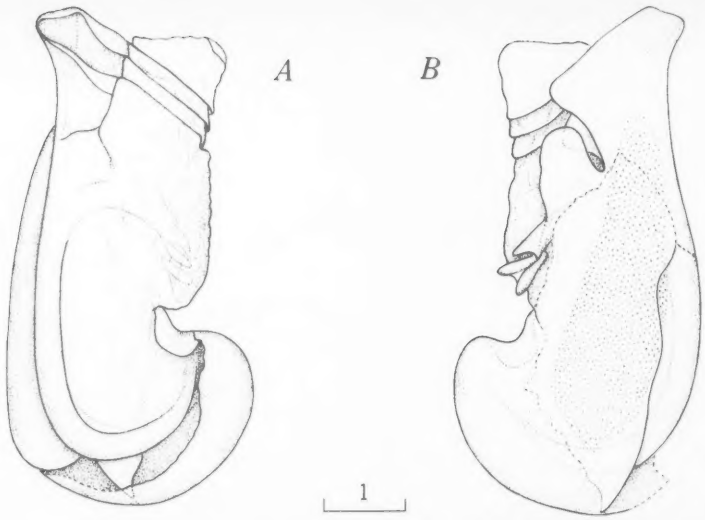

FIGURE 63.—*Mesopenaeus tropicalis*, ♂ 19 mm cl, south of Great Inagua, Bahama Islands. *A*, Left spermatophore dissected from terminal ampulla (wing slightly displaced), ventrolateral view. *B*, Dorsomesial view (dorsal plate removed).

the thelycum. Unlike the release of the sperm masses in certain members of the subgenus *Litopenaeus* (genus *Penaeus*) the sperm appears to be liberated in *M. tropicalis* without a rupture of the spermatophore.

Three females with spermatophores attached were examined by me. The smallest of these specimens, 12 mm cl, was caught off Savannah, Ga., at *Silver Bay* stn 3658. The other two were 19.5 mm cl, and one was taken south of St Vincent Island at *Oregon* stn 896 and the other off Gulf Beach at *Oregon* stn 1254, both localities off northwestern Florida.

Remarks.–In his original brief diagnosis of *Parartemesia tropicalis*, Bouvier (1905b) stated that the species is from the "mer des Antilles," where it had been collected between 80 and 175 fm (146 and 320 m), during a cruise of the *Blake;* he cited neither the number of specimens he had examined nor the locality where they had been found. Later, he (1906b) mentioned the same shrimp (including it among the species of the genus *Haliporus* found in the tropical subtropical Atlantic) as occurring in the "Antilles." However, A. Milne Edwards and Bouvier (1909)—in a rather detailed account of various morphological features of the female of the species, including the thelycum—referred to the same specimen (17.5 mm cl, about 74 mm tl), as the "type," and added the following information: "Habitat, . . .—Blake: Florida Bank, lat. N. 26° 31′, long. O. 85° 03′, 119 brasses.—Le type femelle décrit plus haut." Furthermore, on plate 3, eight figures are explicitly identified as parts of the "type." A. Milne Edwards and Bouvier also recorded and illustrated a smaller female, "25 à 30 mm de longeur" (5.5 mm cl, about 27 mm tl), from Barbados taken in 76 fm (139 m) which, according to a label dated 1907, in Bouvier's handwriting, is a "cotype juvenile," evidently thus designated during the course of the investigations published 2 yr later. The minimum depth of the bathymetric range (80-175 fm) originally given for the species is only slightly greater than that at which the small female was collected, but the maximum depth is considerably deeper than that reported for the larger female, suggesting that the authors had examined additional specimens. Of the material first studied by Bouvier, these two females are the only specimens of this species known to have been taken during cruises of the *Blake* and, furthermore, the small one was identified by Bouvier on a piece of paper accompanying the specimen in the bottle as *Parartemesia tropicalis*, i.e., within the genus proposed in 1905. Consequently, I am convinced that

these two specimens are part of the syntypic series. Inasmuch as the larger female was treated as the type by A. Milne Edwards and Bouvier, I am furthering the latter authors' intent by designating it the lectotype of *Parartemesia tropicalis* [=*Mesopenaeus tropicalis*], and the small female is, therefore, a paralectotype.

The type-locality of *H. tropicalis* is uncertain. A. Milne Edwards and Bouvier (1909) copied the coordinates of *Blake* stn 50 from the label enclosed in the jar with the specimen; I have examined this label and confirmed their data. However, the locality corresponding to those coordinates is beyond the 1,500-fm (2,744-m) contour, and thus considerably deeper than the greatest depths otherwise recorded for this shrimp, a species that penetrates only the shallower portion of the upper slope. Prior to the publication of A. Milne Edwards and Bouvier, the coordinates and depth of *Blake* stn 50 were recorded, in a serial list of *Blake* stations (Anonymous 1879), as follows: 26°31′N, 85°53′W, 119 fm (218 m). Later, S. Smith (1889) quoted the latter data, noting that "The position or depth must be wrong as there are 1700 fm (3109 m) there, perhaps 28°31′." S. Smith's suggestion concerning the latitude was perhaps based on that of the three previous *Blake* stations, which were 28°42′00″N, 28°47′30″N, and 28°51′30″N; however, these are at longitudes greater than 88°W, situated off the Delta of the Mississippi River, and thus far from Florida. The confusion regarding the location of station 50 is even greater, because the name "Florida Bank" is not found on American hydrographic charts, although it can be deduced that A. Milne Edwards and Bouvier referred to West Florida Shelf, the edge of which lies just east of where, according to the label, the specimen was obtained. It seems to me that the type-locality of this species will remain indeterminable.

Under the name *Solenocera weymouthi*, Lindner and Anderson (1941) presented an excellent description of *M. tropicalis*. Two of their statements seem to be in need of modification: only the ventral antennular flagellum is flattened (but not canaliculate), the dorsal one being subflagelliform. The locality given for the allotype is in error. W. L. Schmitt kindly allowed me to examine his logbook of the collections made off the Dry Tortugas in 1932, the time at which the specimen was collected. His records show that "boat sta 74," the locality in question, corresponds to the *Anton Dohrn* trawl haul made 14 miles (22.5 km) south of the Dry Tortugas in 60 fm (110 m) on 5 August 1932. The data given by Lindner and Anderson are those for *Anton Dohrn* station 71, made the same day but, as they quoted, 19.5 miles (31.4 km) south of the Dry Tortugas at 190-280 fm (347.5-512 m).

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The illustrations, a necessary part of this work, were prepared by María M. Diéguez, who once again has applied her artistic talent and painstaking efforts to a better understanding of the American penaeoids, a contribution which I fully appreciate.

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SMALL-SCALE MOVEMENTS OF ALBACORE, *THUNNUS ALALUNGA*, IN RELATION TO OCEAN FEATURES AS INDICATED BY ULTRASONIC TRACKING AND OCEANOGRAPHIC SAMPLING

R. MICHAEL LAURS,[1] HEENY S. H. YUEN,[2] AND JAMES H. JOHNSON[3]

ABSTRACT

Studies with ultrasonic tracking techniques and oceanographic sampling demonstrated that oceanographic conditions play an important role in the local concentrations and movements of albacore, *Thunnus alalunga*, in U.S. coastal waters. Albacore show a tendency to congregate in the vicinity of coastal upwelling fronts, presumably to feed. They move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. The movements of albacore also appear to be related to the distribution of sea surface temperature, with fish spending little time in water with surface temperatures cooler than 15.0°C.

The average swimming speed for three fish tracked between 27.8 and 50 h was 1.6 knots (82.4 cm/s) with each fish exhibiting slightly faster swimming speeds during hours of daylight than during hours of darkness.

The albacore, *Thunnus alalunga* (Bonnaterre), is widely distributed in the Pacific Ocean. The single subpopulation which is found in the North Pacific (Otsu 1960) supports important surface commercial fisheries in coastal waters off North America and Japan and subsurface fisheries in the central temperate Pacific. The species is also highly prized by U.S. recreational fishermen. Passive tagging methods have been used to study large-scale migratory patterns of albacore in the North Pacific (Ganssle and Clemens 1953; Otsu 1960; Clemens 1961, 1963; Otsu and Uchida 1963; Laurs and Nishimoto[4]); however, information on small-scale movements is scant.

In order to examine the small-scale movements of schools of albacore and evaluate the effects that oceanographic conditions may have on the local concentrations and movements of albacore in coastal waters off the United States, studies were conducted with ultrasonic tracking techniques and oceanographic sampling.

Tracking the movements of animals to which ultrasonic transmitters have been attached is a technique that has been developed over the past two decades. This valuable technique has gained such wide application in recent studies of marine fishes and crustacea that it is more convenient to cite a bibliographic source (Stasko 1975) than to cite individual references.

[1]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.
[2]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.
[3]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.
[4]Laurs, R. M., and R. N. Nishimoto. 1974. Joint NMFS-AFRF albacore tagging study. SWFC Admin. Rep. LJ-74-47:63-81.

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METHODS

In the course of acoustic tracking studies, environmental data commonly have been collected for correlation with observed movements of the animal. At times, small auxiliary craft have been used for this purpose in support of the vessel doing the tracking, but usually the collection of environmental data has been done entirely from aboard the tracking vessel, necessarily limiting measurements to the ship's track. This study represents a significant expansion of supportive environmental data acquisition: for the first time a major oceanographic research vessel and an aircraft were coordinated with acoustic tracking of fish. The ultrasonic tracking experiment involved the use of the commercial albacore fishing baitboat *Linda* on charter to the American Fishermen's Research Foundation, the National Marine Fisheries Service (NMFS) RV *David Starr Jordan*, and a Coast Guard aircraft equipped with sea surface temperature measuring equipment.

Capture, Handling, and Tagging of Albacore

The capture of fish, tagging with ultrasonic

transmitters, and tracking of the fish were done aboard *Linda* by three NMFS scientists with assistance from the crew of *Linda*. Albacore ranging in size from 74 to 87 cm fork length with estimated weights of 8.2 to 13.6 kg were caught on hook and line baited with anchovy. The fish was played an average of 5 min before being brought on board by dip net. Without removing it from the net, the fish to be tagged was placed on its side on a plastic covered foam measuring pad on the deck where it was measured to the nearest lower centimeter and the transmitter was attached. A wet burlap bag was placed over its head to keep the fish calm. No anesthetic was used.

The ultrasonic transmitter was attached to the back of the fish, immediately in front of the second dorsal fin, with two sutures through the skin and muscle tissue in that area. Upon completion of tagging, fish were immediately replaced in the water. Total elapsed time for fish out of water was between 1 and 1½ min. Within 2 to 4 s after being released, each tagged fish was observed righting itself and actively swimming downward and out of sight. One fish was tracked at a time. The three fish tracked longer than 24 h were tagged in the manner described above. Several fish tracked for shorter periods early in the cruise were tagged by inserting the transmitter into the stomach through the mouth. This latter method was abandoned when it appeared that acoustic signal attenuation caused by internal implacement was resulting in an inadequate receiving range.

Tracking Equipment

The transmitter tags and hydrophone used were built by the Northwest and Alaska Fisheries Center, Seattle, Wash. The tags were cylindrical measuring 8.2 by 1.9 cm, weighing 67 g in air and 43 g in water, and emitted a 45 or 50 kHz signal at a pulse rate of 120 pulses/min. Acoustic source level of the tag was 63 dB (reference to 1 μbar at 1 m in fresh water).

The hydrophone was a tuned 6-element array (sensitivity - 69 dB, reference to 1 μbar at 1 m) with a beam width of 20° horizontally and 40° vertically at the 3-dB point. This was attached to the lower end of a 3-cm aluminum pipe, bracketed to the starboard rail amidship of the tracking vessel. A geared electric motor at the top of the pipe rotated the hydrophone, which was remotely controlled from the tracking station in the wheelhouse. Signals picked up by the hydrophone were fed into a Lawson VLF-1[5] superheterodyne receiver.

Tracking Procedure

With the hydrophone remote-control unit installed in the pilothouse of *Linda* alongside the engine and steering controls and the receiver placed about 2 m away, one person was able to operate the tracking system and control the vessel simultaneously. Directing the hydrophone for maximum signal, the operator moved the vessel on that heading until satisfied, on a basis of signal strength, with his proximity to the fish. The receiving range varied widely according to sea state, but on the average *Linda* was kept an estimated 500 m from the tagged fish. The fish moved continuously and so, consequently, did the vessel, but vessel speed of more than 2 knots was seldom necessary to keep up with the fish. Position of the tracking vessel was determined approximately once an hour and was taken also to represent the position of the fish at that time. Most of the navigation for *Linda* was done by the nearby *David Starr Jordan*, with a combination of Loran, radar, and Omega systems.

Oceanographic Observations Made From Ship

Detailed oceanographic observations were made aboard *David Starr Jordan* in support of the ultrasonic tracking experiments. These included continuous monitoring of surface temperature and salinity and measurements of subsurface temperature and salinity at selected stations. Observations were also made to evaluate biological factors of the marine environment. These included continuous monitoring at the surface and subsurface measurements at selected stations of chlorophyll a by fluorometric techniques (Holm-Hansen et al. 1965), measurements of primary productivity by ^{14}C methods (Owen and Zeitzschel 1970), and estimates of the standing stocks of potential albacore food organisms.

The estimates of potential albacore forage were derived from hauls made with a 1.8-m Isaacs-Kidd midwater trawl (IKMT) lined with a 58-mm mesh. The hauls were taken during hours of darkness

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

from the surface to a depth of approximately 175 m at a ship speed of about 5 knots. The volumes of water strained were estimated from data obtained by a TSK[6] depth-distance recorder mounted in the mouth of the trawl. The Formalin-preserved IKMT catches were sorted into several categories of fishes, cephalopods, crustaceans, and other animals, and the displacement volume of each of these kinds of animals was measured and standardized in ml/1,000 m^3 of water filtered for each haul. The standardized values of 1) larval and juvenile fishes, 2) epipelagic fishes, 3) cephalopods, and 4) crustaceans were summed for each haul and collectively regarded as potential albacore forage. Analysis of stomach contents of albacore has shown that these categories of organisms are important in the diet of albacore (Pinkas et al. 1971) in this area.

Oceanographic Observations Made by Aircraft

A Coast Guard aircraft equipped with a Barnes PRT-5 infrared radiometer made measurements of sea surface temperature for evaluation of the small-scale features and changes in the distribution of sea surface temperature.

RESULTS AND DISCUSSION

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from about 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). Results will be presented for fish numbers 4, 5, and 6, which were tracked for 27.8, 41.4, and 50.0 h, respectively. There are too few data for discussion for fish numbers 1, 2, and 3 because of the short periods that the fish were tracked. A summary of the tracking date and time, tagging location, distance tracked, and fork length of fish for fish numbers 4, 5, and 6 is given in Table 1.

Tagged fish rejoined untagged albacore after being returned to the water, and tended to remain in their company. Surface "boils" characteristic of albacore were frequently sighted close by *Linda*, and approximately 30 fish of the same general size as fish tagged with ultrasonic transmitters were caught by the crew while tracking was in progress. Also, one tagged fish "lost" the previous day was heard intermittently over a 4-h period during the track that followed. We were able to distinguish between the two fish because of slightly different signals from the tags.

[6]Tsurumi Seiki Kosakusho Co., Ltd., Yokohama, Japan.

TABLE 1.—Summary of tracking date and time, fork length of albacore, location of tagging, and distance tracked.

No.	Date	Time	Fork length	Tagging location Lat.	Long.	Distance
4	8-16-72 to 8-17-72	1445 to 1845	84 cm	36°49.8'N,	122°19.1'W	41.6 nmi (77.1 km)
5	8-19-72 to 8-20-72	0715 to 2345	87 cm	36°50.3'N,	122°13.6'W	61.4 nmi (113.8 km)
6	8-25-72 to 8-27-72	1000 to 1205	85 cm	35°20.0'N,	121°22.0'W	81.3 nmi (150.7 km)

Speed of Albacore Movements

Swimming speeds for albacore were estimated from straight-line calculations using position of the tracking vessel. The average swimming speed, based on the total distance and time that the fish were tracked, for fish numbers 4, 5, and 6 was about 1.6 knots (82 cm/s). Speeds calculated from hourly ship positions for each fish ranged from 0.1 to 3.6 knots (5 to 185 cm/s). Table 2 shows the percentage of time each fish spent at various swimming speeds. There were day-night differences in the rate of movement, with fish exhibiting faster swimming speeds during hours of daylight (0500 to 1900 h) than during hours of darkness. The average speed during daylight for fish numbers 4 and 5 was 1.7 knots (88 cm/s) and for number 6 was 2.1 knots (108 cm/s). The average speed during nighttime for fish numbers 4 and 6 was 1.3 knots (67 cm/s) and for fish number 5 was 1.0 knot (51 cm/s). Table 3 gives a summary of time, distance, and mean speeds.

Moonlight also appeared to influence the rate of movement of fish number 5. This fish, which had been moving steadily at about 2.0 knots (103 cm/s) for about 3 h after moonrise and following a course about 20° west of the full moon, came to a near stop

TABLE 2.—Percent of time each albacore spent at various swimming speeds.

Speed		Fish no. 4	Fish no. 5	Fish no. 6
knots	cm/sec		Percent	
<0.5	<26	8.0	5.9	0.0
0.5-0.9	26- 46	12.0	23.5	15.8
1.0-1.4	51- 72	32.0	35.3	28.9
1.5-1.9	77- 98	24.0	11.8	15.8
2.0-2.4	103-124	16.0	17.6	28.9
2.5-2.9	129-149	4.0	2.9	0.0
3.0-3.4	154-175	0.0	2.9	10.5
>3.5	>175	4.0	0.0	0.0

TABLE 3.—Summary of duration and distance tracked and mean speed of albacore tracked with ultrasonic transmitters.

Item	Fish no. 4	Fish no. 5	Fish no. 6
Time tracked (h)	27.8	41.4	50.0
Distance tracked:			
nmi	41.6	61.4	81.3
km	77.1	113.8	150.7
Mean speed:			
knots	1.6	1.5	1.6
cm/s	82	77	82
bl/s[1]	0.98	0.88	0.96
Mean speed, day:[2]			
knots	1.7	1.7	2.1
cm/s	88	88	108
bl/s[1]	1.05	1.01	1.27
Mean speed, night:[3]			
knots	1.3	1.0	1.3
cm/s	67	51	67
bl/s[1]	0.80	0.59	0.79

[1]bl/s = body lengths per second.
[2]0500-1900 h.
[3]1900-0500 h.

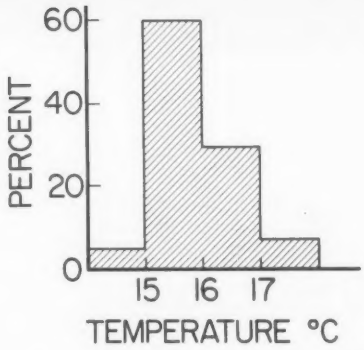

FIGURE 1.—Percent of time (hours) spent in waters of various sea surface temperature by albacore numbers 4, 5, and 6.

for nearly an hour when the moon was suddenly obscured by dense fog at about 0300 h.

The mean swimming speeds calculated from the tracking experiment are close to estimates of swimming speed derived from passive tagging results. For example, based on data given in the Japanese Fisheries Agency (1975) report, two tagged albacore, which were released in the western North Pacific and recovered in the eastern North Pacific about 3½ mo later, traveled at 1.1 knots (57 cm/s), assuming they followed a great circle route and were caught the day they arrived at the recovery location. The mean swimming speeds found in this study are slightly less than twice the calculated minimum swimming speed necessary for an 80-cm albacore to maintain hydrostatic equilibrium (Dotson 1977).

Relationship of Albacore Movements to Sea Surface Temperature

The movements of the fish tagged with ultrasonic transmitters appeared to be influenced by the distribution of sea surface temperature. Figure 1 shows the percentage of the time that fish numbers 4, 5, and 6 spent in waters of various surface temperatures. Fish number 6 spent no time in water with surface temperatures less than 15.0°C although roughly 20% of the waters 5 nmi distant on both sides of the path followed by the fish were colder than 15.0°C. Fish number 4 was in water which had surface temperatures colder than 15.0°C 12.5% of the time, while 35% of the waters 5 nmi distant on both sides of the path followed by the fish was colder than 15.0°C. Fish number 6 was in water with surface temperatures warmer than 17.0°C 22% of the time, which coincided with the percentage of area with temperatures greater than 17.0°C. Water with temperature higher than 17.0°C was not available to fish numbers 4 and 5.

These results indicate that the transmitter-tagged fish spent very little time in water with surface temperatures less than 15.0°C. This is especially evident when charts showing the tracks followed by the fish and the contoured field of sea surface temperature observed by *David Starr Jordan* at the time of tracking are examined. Figures 2, 3, and 4 show tracks followed by fish numbers 4, 5, and 6, respectively, and sea surface temperature. In these figures, temperatures less than 15.0°C, which are considered below the habitat preference for albacore (Clemens 1961), are shaded. Fish number 4 remained in the vicinity of a band of water cooler than 15.0°C for nearly the total time it was tracked, but did not appear to enter it (Figure 2). Fish number 6 traveled on a southerly course, in a corridor of warm water which was sandwiched between two wedges of cool water on 25 August, but did not enter the cool water on either side except very briefly at the start of tracking (Figure 4). When the fish passed to the south of the cool water, where there was a large area of water warmer than 15.0°C, the fish changed its direction generally to a more southwesterly course.

Relationship of Albacore Movements to Upwelling Temperature Fronts

A well-developed temperature front occurs at the boundary between cool, biologically rich

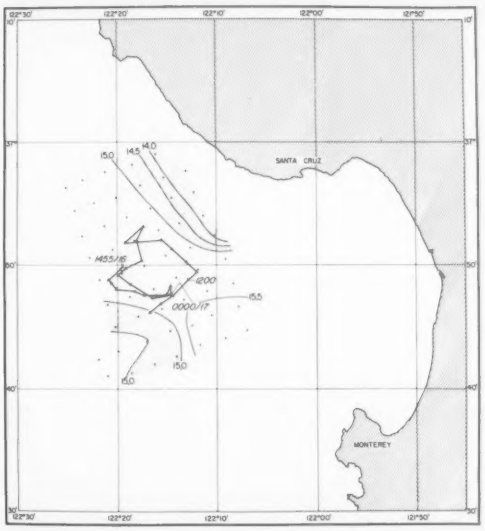

FIGURE 2.—Movements of albacore number 4 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.

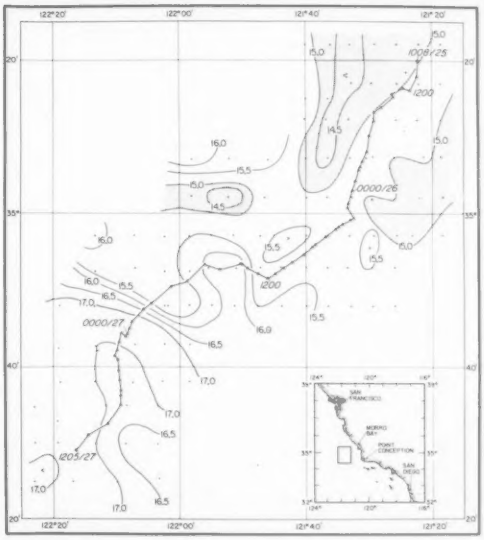

FIGURE 4.—Movements of albacore number 6 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.

upwelled water and warmer, nonupwelled water (Smith 1968). The effects that an upwelling front may have on the movements of albacore were indicated during the ultrasonic tagging experiment. On 17 August, during tracking operations for fish number 4, a relatively well-developed upwelling surface temperature front was observed in the northeast portion of the tracking area. The upwelling was caused by brisk northerly winds which had been blowing for several days. The remainder of the area surveyed has a rather simple surface temperature distribution mostly within the temperature range considered as the habitat preference for albacore (Figure 2).

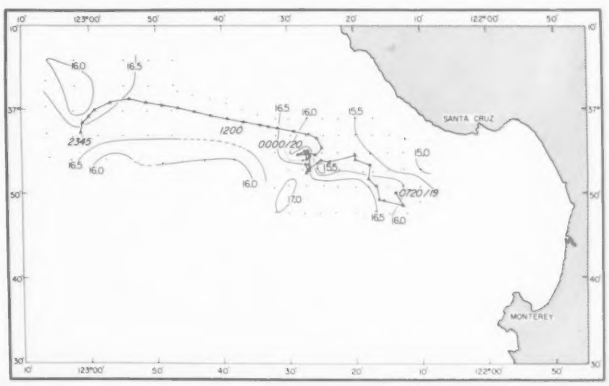

FIGURE 3.—Movements of albacore number 5 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*.

Infrared radiation temperature measurements made during an overflight by the Coast Guard aircraft on 16 August showed that the water on the cold side of the front continued to decrease toward shore to values below 13.0°C.

Fish number 4 traveled in about an 8 × 8 nmi area on the warm side of the upwelling front and in close proximity to it for nearly the total time the fish was tracked. Subsequently, high winds and rough seas made tracking difficult and the signal from the fish was lost during hour 27 of tracking.

Fish number 5 exhibited a much different pattern of movement than did number 4 (compare Figures 2 and 3). It moved many miles from the location where it had been tagged, in a general northwesterly direction, rather than remaining in the local vicinity as fish number 4 had done.

Examination of oceanograhic data revealed that marked changes in the distribution of sea surface temperature had occurred between 17 and 19 August (compare Figures 2 and 3). Upwelling had subsided, the upwelling temperature front was no longer present on 19 August, and the temperature over much of the area had increased by about 1.5°C. The breakdown of the upwelling front and warming was due to a slackening and shifting of the winds to a westerly-southwesterly direction which allowed a thin layer of warmer offshore water to flow toward the coast.

It is presumed that the school of fish with which fish number 4 was traveling remained in the vicinity of the upwelling front to feed in the highly productive water associated with the upwelling. Measurements of chlorophyll were high in the tracking area and showed a very strong positive gradient on the cold side of the upwelling front (Figure 5). Measurements of ^{14}C uptake indicated a primary production rate integrated over the euphotic zone (0 to 36 m) of 1,511 mg C/m² per day. The biomass of potential albacore food organisms was also high, ranging from about 20 to 56 ml/1,000 m³ water strained, in midwater trawl collections made at night in the nearby area where tracking took place (Table 4).

Albacore were frequently seen boiling in the area nearby the upwelling front by personnel aboard *Linda* and *David Starr Jordan*. Also, observers aboard the Coast Guard aircraft noted about 25 to 30 commercial albacore jig boats fishing immediately on the warm side of the front in water warmer than 15.0°C. High biological production in the area of the upwelling front was also indicated by large numbers of sea birds and numerous sightings of marine mammals, including blue whales and other whales.

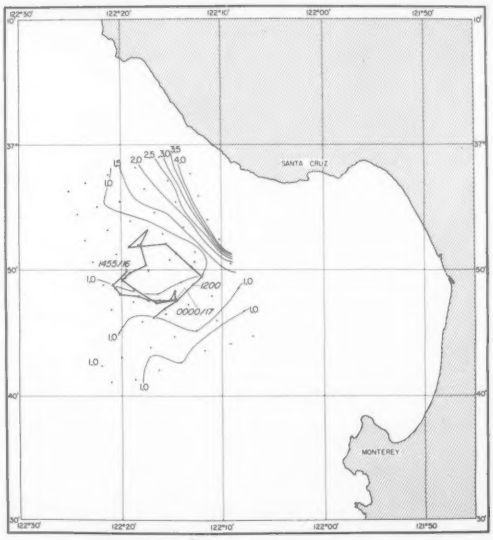

FIGURE 5.—Movements of albacore number 4 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

TABLE 4.—Summary of dates, times, positions, and estimates of potential albacore forage, 1972.

Fish no.	IKMT no.	Date	Time	Lat. (N)	Long. (W)	Forage biomass (ml/1,000 m³)
4	1	15 Aug.	2200-2240	36°50′	122°14′	28.8
	2	16 Aug.	2159-2238	36°47′	122°15′	36.2
	3	17 Aug.	2137-2215	36°55′	122°24′	56.2
	4	18 Aug.	0032-0111	36°53′	122°16′	51.5
	5	18 Aug.	0130-0210	36°52′	122°19′	30.4
	6	18 Aug.	0232-0311	36°49′	122°22′	37.7
	7	18 Aug.	0352-0430	36°50′	122°11′	30.7
	8	18 Aug.	0516-0553	36°41′	122°19′	29.8
5	9	21 Aug.	2116-2150	37°06′	122°50′	5.7
	10	21 Aug.	2236-2314	36°57′	122°59°	10.1
	11	22 Aug.	0032-0115	36°54′	122°38′	24.5
	12	22 Aug.	0152-0231	36°48′	122°30′	23.1
	13	22 Aug.	0302-0341	36°55′	122°25′	10.6
	14	22 Aug.	0412-0450	36°52′	122°17′	24.9
6	15	27 Aug.	2119-2156	34°40′	122°14′	5.8
	16	27 Aug.	2241-2320	34°48°	122°02′	8.0
	17	28 Aug.	0040-0122	34°53′	121°51′	5.9
	18	28 Aug.	0214-0251	35°07′	121°29′	10.1
	19	28 Aug.	0325-0402	35°15′	121°26′	19.6

It is possible that fish number 5 and the school it was traveling with left the immediate area where it had been tagged because food organisms were no longer concentrated there due to the breakdown of the upwelling front. This explanation is supported by the observation on 19 August of an overall reduction in the concentration of surface

FIGURE 6.—Movements of albacore number 5 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

chlorophyll a, as much as three to four times lower in waters where upwelling had been taking place on 17 August (Figure 6). Also, measurements of ^{14}C uptake indicate that the rate of primary production was about 33% lower, 1,014 mg C/m^2 per day, than it had been when fish number 4 was tracked. In addition, estimates of biomass of potential albacore forage organisms taken in midwater trawl hauls made during tracking operations for fish number 5 were less, ranging from about 6 to 25 ml/1,000 m^3 of water filtered (Table 4), than during tracking operations for fish number 4. (Relatively low chlorophyll a values (Figure 7) and albacore forage biomass values (Table 4) were also observed during tracking operations for fish number 6.)

While tracking information on only two fish does not provide sufficient data from which to make generalizations, the results suggest that 1) albacore concentrate in the vicinity of upwelling fronts, presumably to feed, and 2) albacore move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. Pearcy and Keene (1974) discussed the possibility of albacore congregating in the region of upwelling fronts. The concentration of albacore in the vicinity of upwelling fronts has also been indicated by high catch rates made by fishing and research vessels near upwelling fronts (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973).

Relationship of Albacore Movements to Other Sea Surface Temperature Fronts

During the tracking operations, it appeared that fish numbers 5 and 6 tended to slow down

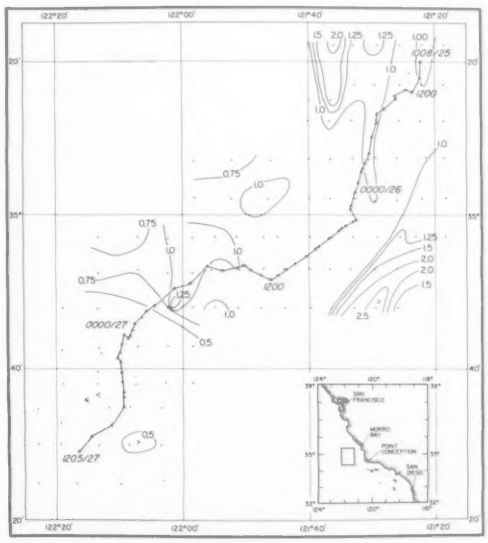

FIGURE 7.—Movements of albacore number 6 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

when crossing temperature fronts where the temperatures on both sides of the front were within the favorable range for albacore. To examine this more closely, mean speeds were estimated for tagged fish when they were within a 5-nmi distance before crossing and after crossing the temperature front and when crossing the front. A sea surface temperature front was defined as a change in surface temperature of 0.5°C or larger in a nautical mile (0.003°C/m). The results are summarized in Table 5 and show that for the three cases examined, 1) the mean speed was slower when crossing the front than it was before

TABLE 5.—Mean speed crossing temperature front[1] and mean speed within 5-nmi radius before and after.

Item	Fish no.	Date	Time	Total (h)	Total distance (nmi)	(km)	Mean speed (knots)	(cm/s)
Before	5	8/19	1330-1600	2.5	5.0	9.3	2.0	103
At front	5	8/19-20	1600-0300	11.0	7.8	14.4	0.7	36
After	5	8/20	0300-0800	5.0	7.0	13.0	1.4	72
Before	6	8/26	1700-1900	2.0	5.6	10.4	2.8	144
At front	6	8/26	1900-2100	2.0	3.7	6.9	1.8	93
After	6	8/26-27	2100-0200	5.0	8.0	14.8	1.6	83
Before	6	8/26	0800-1230	4.5	6.1	11.3	1.4	72
At front	6	8/26	1230-1400	1.5	2.0	3.7	0.7	36
After	6	8/26	1400-1600	2.0	5.2	9.7	2.6	134

[1] ΔT = 0.5 C/1.0 nmi.

crossing the front in all three cases, and 2) the mean speed was slower when crossing the front than after crossing the front in two cases. These data should be viewed with caution, however, because in two instances, daytime and nighttime data were used together and some of the differences in speed may be due to variation associated with time of day. The relationship did hold up well in the single case when daytime data only were used.

We think the changes in swimming behavior observed at temperature fronts reflected perception and response to the increased temperature gradient per se. In the case of the alteration in the swimming pattern of fish number 5 as it encountered a temperature front at lat. 36°53′N, long. 122°27′W (Figure 3), there was no sharp gradient in any of the other environmental parameters we measured.

That tunas can perceive abrupt temperature changes as small as 0.1°C has been demonstrated by Steffel et al. (1976) for captive kawakawa, *Euthynnus affinis*. Moreover, a mechanism has recently been suggested (Neill et al. in press) whereby tunas might be able to orient themselves in temperature gradients much gentler than those of our fronts, perhaps even as slight as 0.0001°C/m; this speculative mechanism invokes the large thermal inertia of tunas as a device for thermal "memory."

Movements of Albacore in Relation to Vertical Thermal Structure

The availability of albacore in offshore waters has been shown to be related to vertical thermal structure (Laurs and Lynn[7]). However, no obvious relationship was observed in this study between the movements of sonic-tagged albacore in coastal waters and subsurface temperature structure. This may be due to the complicated vertical temperature structure that was observed in the areas where fish were tracked and the lack of data on the depth of the fish.

SUMMARY

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). The average swimming speed for these fish tracked between 27.8 and 50.0 h was 1.6 knots (82 cm/s) with each fish exhibiting slightly faster swimming speeds during the day than during the night. The mean swimming speeds observed during the tracking experiment are similar to estimates of swimming speed derived from passive tagging results and about twice the calculated minimum swimming speed necessary to maintain hydrostatic equilibrium.

The tracking experiment indicated that oceanographic conditions may play an important role in the local concentrations and movements of albacore in coastal waters. The movements of fish appeared to be related to the distribution of sea surface temperature, with transmitter-tagged fish spending very little time in water with surface temperatures less than 15.0°C. The results also indicate that upwelling temperature fronts may markedly influence the local concentration of albacore, with albacore tending to concentrate in the vicinity of upwelling fronts, presumably to feed, and moving away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. There was also some indication that albacore tended to slow down when crossing sea surface temperature fronts

[7] Laurs, R. M., and R. J. Lynn. 1974. The offshore distribution and availability of albacore during early-season and the migration routes followed by albacore into North American waters. SWFC Admin. Rep. LJ-74-47:19-46.

where the temperatures on both sides of the front were within the optimal range for albacore.

Finally, the tracking experiment demonstrated that acoustic tracking of albacore is feasible and that it can be a useful tool in studies designed to understand better the relationships between albacore and the marine environment.

ACKNOWLEDGMENTS

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ANNUAL FLUCTUATIONS IN BIOMASS OF TAXONOMIC GROUPS OF ZOOPLANKTON IN THE CALIFORNIA CURRENT, 1955-59

J. M. COLEBROOK[1]

ABSTRACT

Year-to-year fluctuations in the abundance of the zooplankton of the California Current region, from 1955 to 1959, have been studied. The abundance of zooplankton was measured in terms of the biomass of each of 17 major taxonomic categories (generally Class or Order). Principal components analysis was used to produce concise descriptions of the major elements of the fluctuations in the abundance of the categories in each of 14 areal subdivisions of the survey area. Considerable coherence with respect to annual changes was found both between the taxonomic categories and between the areas. The principal common element in the fluctuations could be associated with a marked increase in the temperature of the surface waters which occurred in 1957 and persisted through 1958 and 1959. A less pronounced but still quite clear common element in the fluctuations could be associated with year-to-year fluctuations in the amount of coastal upwelling in the area.

Since 1949, the regular surveys conducted by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program have yielded information about a variety of physical, chemical, and biological parameters (see, e.g., Marine Research Committee 1957). For the CalCOFI survey cruises during January, April, July, and October for each of the years from 1955 to 1959, samples of zooplankton were analyzed to provide estimates of the biomass for each major taxonomic category within the zooplankton (Isaacs et al. 1969).

These data were generously made available to the author by J. D. Isaacs to provide material for a study of year-to-year changes in the abundance of the major components of the zooplankton. As stated by Isaacs et al. (1969), "Selection of the years 1955 through 1959 for analysis of biomass distribution was dictated by interest in the occurrence and nature of patterns of seasonal and annual variability among the functional groups of zooplankton. During this time, yearly mean temperatures above the thermocline shifted upward from the relatively cold years of 1955 and 1956 to the relatively warm years of 1958 and 1959."

The object of the study described in this paper is to describe the annual changes, from 1955 to 1959, in the abundance of the zooplankton of the CalCOFI survey area in as much detail as is available from the survey data in order to discover whether observed changes can be associated with environmental fluctuations.

MATERIAL

The details of the procedures for deriving biomass estimates have been described by Isaacs et al. (1969), who also give the reasons for the selection of the particular set of taxa (listed in Table 1). It was their intention to provide estimates of the "nutrient quality" of the standing crop of zooplankton as well as an index of "trophodynamic complexity." The categories were chosen to represent the quality and quantity of zooplankton as food for fish rather than as indicators of variability of the zooplankton as such.

TABLE 1.—A list of the taxa from CalCOFI cruises for which biomass estimates are available. They are listed in alphabetical order and a code used in Figures 7 and 10 is given.

Taxa	Code	Taxa	Code
Amphipoda	AMPH	Larvacea	LARV
Chaetognatha	CHET	Medusae	MEDS
Cladocera	CLAD	Mysidacea	MYSD
Copepoda	COPD	Ostracoda	OSTR
Crustacea larvae	CRST	Pteropoda	PTER
Ctenophora	CTEN	Radiolaria	RADL
Decapoda	DECP	Siphonophora	SIPH
Euphausiacea	EUPH	Thaliacea	THAL
Heteropoda	HETP		

The collection method for the standard CalCOFI plankton samples has been described in

[1]Institute for Marine Environmental Research, Plymouth, England.

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detail by, e.g., Ahlstrom (1954) and Fleminger (1964). Very briefly, the net is 1 m in diameter at the mouth and 5 m long, the filtering section having a mesh size of about 0.5 mm. The net is towed obliquely, from a ship traveling at a speed of about 2 knots, from the surface down to a depth of 140 m and then returned to the surface. The volume of water fitered varies from about 400 to 600 m^3.

Charts of the distribution of biomass for each taxon have been given by Isaacs et al. (1969) for the April and October cruises, by Isaacs et al. (1971) for the January cruises, and by Fleminger et al. (1974) for the July cruises. The station data are held on a magnetic tape file at the Southwest Fisheries Center, National Marine Fisheries Service.

DATA PROCESSING METHODS

For the purposes of presenting summaries of CalCOFI data in a compact form and to permit some smoothing of the data by taking average values, P. E. Smith's proposal for subdividing the survey area into 23 zones was used in this study (Figure 1). The extent of the survey and hence the number of stations occupied varied from cruise to cruise. The station patterns for the cruises included in this study are given in Smith (1971), and a summary showing the numbers of samples in each zone is given in Table 2.

The biomass data are available as grams/1,000 m^3 and estimated to two decimal places. The range of estimates is from zero to over 5,000 g, and within each taxon they are heavily positively skewed.

The results presented here were expressed in terms of relative changes in biomass in time and space within each taxonomic category, and extensive averaging was employed. It was decided, therefore, to apply a logarithmic transformation to the original estimates. Averages based on log transformed values are weighted in favor of the more numerous low values as opposed to arithmetic means, the values of which may be determined largely by small numbers of high estimates.

In order to give zero a value on the transformed scale it is normal to add 1 to the observation prior to transformation. In this case, where the biomass has been estimated to two decimal places, a number of options is available, either 1.0, 0.1, or 0.01 can be added prior to transformation. Trials

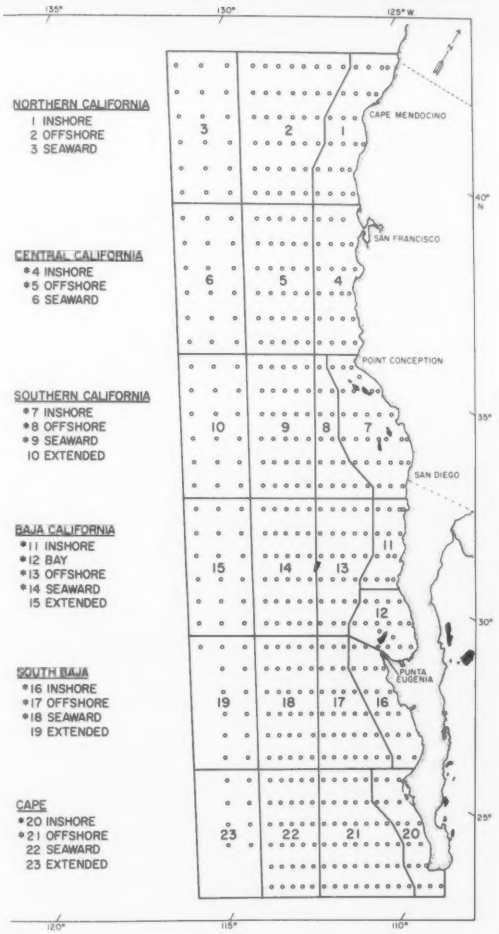


FIGURE 1.—A chart of the area of the CalCOFI survey showing the grid of station positions on which were based the cruises during the period 1955-59. Also shown is the subdivision of the area into the standard zones used in this study. The well-sampled zones for which annual means of biomass were calculated are marked with an asterisk (see Table 2).

involving the calculation of means for each zone for each cruise for a subset of the taxonomic categories indicated that adding 1.0 produced a considerable loss of resolution for means corresponding to less than 1 g/1,000 m^3, and adding 0.01 produced a resolution of low means that appeared to be greater than was warranted by the accuracy of the data. Therefore throughout this study a transformation of the form

$$Y = \log_{10}(10X + 1)$$

TABLE 2.—The numbers of samples collected during each of the January (Jn), April (Ap), July (Jl), and October (Oc) CalCOFI cruises for the years 1955-59 in each of the standard zones (see Figure 1). Annual totals are given in boldface and the grand total is printed in italic.

	1955					1956					1957					1958					1959					
Zone	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Grand total
Central California:																										
Inshore	0	0	13	13	**26**	0	18	16	0	**34**	0	0	16	0	**16**	9	21	23	20	**73**	15	20	24	18	**77**	*226*
Offshore	0	0	9	6	**15**	0	9	18	0	**27**	0	0	10	0	**10**	2	21	20	17	**60**	12	14	30	18	**74**	*186*
Southern California:																										
Inshore	20	17	27	22	**86**	21	22	29	27	**99**	0	25	26	26	**77**	18	27	26	29	**100**	29	28	28	27	**112**	*474*
Offshore	4	6	14	6	**30**	4	6	13	9	**32**	0	7	12	6	**25**	5	13	14	9	**41**	6	12	14	9	**41**	*169*
Seaward	3	17	20	6	**46**	5	13	26	6	**55**	0	17	23	17	**57**	11	21	27	17	**76**	11	30	29	17	**87**	*321*
Baja California:																										
Inshore	12	12	13	12	**50**	12	12	14	0	**38**	8	13	12	13	**46**	12	13	11	13	**49**	13	14	13	14	**54**	*237*
Bay	12	13	14	11	**50**	11	12	15	0	**38**	12	15	16	14	**57**	10	16	14	16	**56**	15	16	17	16	**64**	*265*
Offshore	11	13	26	4	**54**	11	11	22	0	**44**	10	20	26	11	**67**	10	25	25	18	**78**	18	26	24	16	**87**	*330*
Seaward	4	12	24	5	**45**	6	16	20	0	**42**	2	16	19	13	**50**	10	30	23	18	**81**	18	29	29	18	**94**	*312*
South Baja:																										
Inshore	16	15	16	14	**61**	13	13	14	0	**40**	16	15	17	17	**65**	15	16	17	17	**65**	17	11	19	17	**64**	*295*
Offshore	8	12	13	6	**39**	8	8	13	0	**29**	8	21	18	12	**59**	12	22	19	20	**73**	19	17	27	20	**83**	*283*
Seaward	3	2	2	3	**10**	1	2	2	0	**5**	1	12	13	13	**39**	3	15	6	7	**31**	8	7	12	8	**35**	*120*
Cape:																										
Inshore	15	0	0	0	**15**	16	16	0	0	**32**	0	19	0	0	**19**	17	0	0	17	**34**	20	10	0	0	**30**	*130*
Offshore	1	0	0	0	**1**	1	10	0	0	**11**	0	22	0	0	**22**	10	0	0	24	**34**	31	14	0	0	**45**	*113*

has been employed. By this transformation, means corresponding to greater than about 0.2 g/1,000 m^3 are virtually on a logarithmic scale while lower means show a progressive transition to an arithmetic scale.

Quarterly means were calculated by averaging the data for the stations in each zone and then these were averaged to give annual values. For those occasions when less than five stations were occupied in any zone, the station data were ignored and a quarterly mean was interpolated by the following method:

1. For each taxonomic category the set of overall zone means (the sum of all the observations for all the cruises in each zone divided by the total number of stations occupied in the zone) was calculated. The set of overall quarterly means (the sum of all the observations for all the cruises in each quarter divided by the number of stations in each quarter) was calculated.
2. For each missing value the sum of the remaining means for the other zones for the cruise and the sum of the corresponding overall zone means were calculated. The latter was weighted by the ratio of the relevant overall quarterly mean to the grand mean and the missing value then calculated as the product of the remaining zone means for the cruise and the weighted sum of the overall zone means.

From these quarterly means, annual means were calculated for each taxon for each of a set of regularly sampled zones (those marked with an asterisk in Figure 1); and principal components analysis was used to extract from these data the main patterns of year-to-year change in biomass. This is a technique of multivariate analysis (see, e.g., Kendall 1957) which generates a sequence of variables known as components with, in this case, values for each year, which are the weighted sums of the standardized data variables, in this case sets of annual means of the taxonomic categories. The sets of weighting factors, with values for each taxonomic category, are the successive latent vectors of the correlation matrix derived from the original data, in this case the table of correlations between the annual variations in abundance of all possible pairs of taxonomic categories. The first latent vector generates a component which has the largest possible variance. The second vector generates a component which has the largest possible variance in relation to the residual following the removal of the variability associated with the first component, and so on. If the original data are coherent to any extent, it is normal for the first few components to account for a large proportion of the variability of the original data array.

GEOGRAPHICAL DISTRIBUTIONS

To provide some geographical background to the study of year-to-year changes in biomass, charts of the overall mean for each taxon in each standard zone were prepared. In order to search

for possible relationships between the geographical distributions of the taxonomic categories, these data were subjected to a principal components analysis.

Figure 2 is a graph of the first latent vector plotted against the second. The graph has a point for each taxonomic category, and the disposition of points represents in a spatial form the relationships between the geographical distributions of the taxonomic categories with respect to the first two components which, in this case, account for 61% of the variability of the original geographical distributions. The interrelationships are probably best regarded in the form of a more or less circular sequence; only the point for Medusae falls well off the sequence.

Figure 3 shows charts of the first two components. The first component shows a very clear north to south, alongshore gradient; and the second shows an equally clear inshore to offshore gradient, indicating that the sequence of categories in Figure 2 runs from categories with northern distributions (Siphonophora to Radiolaria) to inshore distributions (Euphausiacea to Cladocera) to southern and inshore distributions (Larvacea to Mysidacea) to offshore distributions (Heteropoda to Ostracoda). Figure 4 shows the distributions of the taxonomic categories arranged in this sequence. They are based on averages of the transformed data, for each zone, for each quarterly cruise for the period 1955-59, excluding zones for which fewer than five stations were occupied. These distributions show variability other than that involved in their relationships with the first two components; nevertheless, the north to inshore to south to offshore sequence can be seen fairly clearly. Heteropods and Pteropods are firmly placed in the sequence of taxonomic categories in the vector plot in Figure 2. They have, however, fairly low values compared with the other categories, and only parts of their distributions conform with the south to offshore transition indicated by their position in the vector plot. The distribution of Medusae (Figure 4) can be seen to include areas of relatively high biomass both in the north and in the south, and clearly it does not fit into the sequence of the other categories.

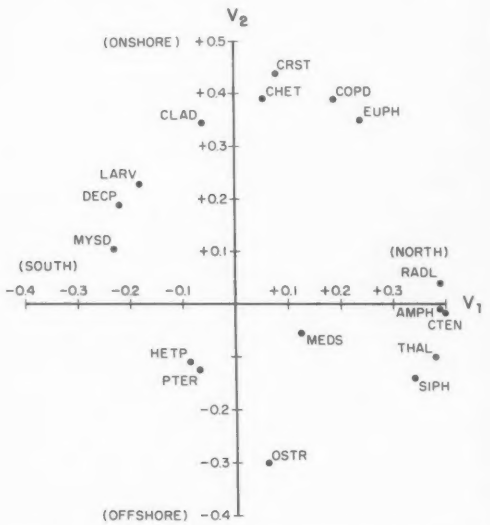


FIGURE 2.—A plot of the first vector against the second vector derived from a principal components analysis of the geographical distributions of the taxa. A key to the abbreviations of the names of the categories is given in Table 1.

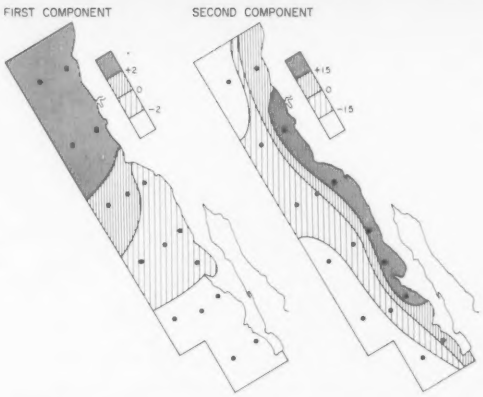


FIGURE 3.—Charts of the first and second components derived from a principal components analysis of the geographical distributions of the taxa.

It is obviously unrealistic to attempt to classify the internally diverse taxonomic categories used here in terms of geographical distribution types such as Brinton (1962) found for Euphausiacea. Brinton found that the alongshore axis of the California Current in the CalCOFI survey area was characterized by transitions from "subarctic" species in the north to "transition" species in the region between lat. 30° and 40°N to "equatorial" species in the south. "Central" species occurred offshore and some "boundary" species occurred inshore in the area. McGowan (1971) has shown

that these patterns are reflected generally in the distribution of the plankton of the Pacific Ocean. It may, nevertheless, be significant that the pattern of distribution of the taxonomic categories reflects both the alongshore and the inshore-offshore transitions in the distribution of the Euphausiacea.

YEAR-TO-YEAR FLUCTUATIONS IN BIOMASS

Annual means of biomass were calculated, as described above, for each taxonomic category (Table 1) for each of the well-sampled standard zones (Figure 1) for each of the years 1955-59. Two sets of principal components analyses were carried out, firstly for each of the 14 standard zones on the annual fluctuations in biomass of each taxonomic category and secondly for each taxonomic category on the annual fluctuations in abundance in each of the standard zones. The same data are involved in both sets of analyses.

Graphs of the first principal components for each of the zone analyses are given in Figure 5. Table 3 shows that these components accounted for between just under one-half and about three-quarters of the total variability; it also shows that all but a very few of the categories showed positive relationships with the components. The graphs show considerable similarity between the various zones. These results indicate that a large element of the year-to-year fluctuation in biomass is common to all the zones and to a vast majority of the taxonomic categories. Nearly all the zones show a relatively high biomass (relative to a mean of zero) in 1955 and 1956 and a low biomass in 1958 and 1959. The data for 1957 vary from zone to zone, perhaps tending to be higher in the northern and offshore zones and lower in some of the southern and inshore zones.

A table was prepared of the corresponding vectors with the taxonomic categories arranged, by trial and error, to give the high positive terms at the top, and the low positive and the few negative terms at the bottom of the table. The final ranking of categories and the vector values are given in Table 4. This rank was compared with the rank of taxa based on the relationships between their geographical distributions (Figure 2) starting with the northern distributions, with Siphonophora and Thaliacea, working round the sequence and ignoring Medusae (also left out of Table 4) to finish with Pteropoda and Ostracoda.

TABLE 3.—For each zone (a) the percentage of the total variability of the original data accounted for by the first component and (b) the number of taxa with positive first vector values (maximum = 17). The code names for the zones used in Table 4 and Figures 6 and 9 are also given.

Zone	Code	a	b
Central California:			
Inshore	CCALIN	74	17
Offshore	CCALOF	71	17
Southern California:			
Inshore	SCALIN	63	14
Offshore	SCALOF	58	17
Seaward	SCALSW	58	15
Baja California:			
Inshore	BCALIN	70	15
Bay	BCALBY	66	16
Offshore	BCALOF	52	14
Seaward	BCALSW	48	13
South Baja:			
Inshore	SBAJIN	64	16
Offshore	SBAJOF	56	16
Seaward	SBAJSW	45	12
Cape:			
Inshore	CAPEIN	54	15
Offshore	CAPEOF	53	16

TABLE 4.—The first vectors of principal component analyses for each standard zone with the taxonomic categories ranked as described in the text. Also the rank of the categories derived from Figure 2.

Taxa	CCALIN	CCALOF	SCALIN	SCALOF	SCALSW	BCALIN	BCALBY	BCALOF	BCALSW	SBAJIN	SBAJOF	SBAJSW	CAPEIN	CAPEOF	"Atlas" rank
Copepoda	0.28	0.28	0.30	0.31	0.36	0.29	0.29	0.30	0.34	0.30	0.30	0.31	0.27	0.30	7
Thaliacea	0.27	0.27	0.30	0.28	0.31	0.28	0.29	0.32	0.33	0.29	0.31	0.29	0.30	0.31	2
Amphipoda	0.27	0.28	0.30	0.32	0.31	0.27	0.28	0.31	0.33	0.28	0.28	0.22	0.29	0.28	4
Siphonophora	0.27	0.28	0.22	0.29	0.23	0.29	0.29	0.25	0.29	0.28	0.30	0.32	0.28	0.28	1
Radiolaria	0.28	0.27	0.30	0.29	0.31	0.28	0.28	0.30	0.28	0.23	0.28	0.20	−.02	0.00	5
Ctenophora	0.26	0.27	0.30	0.26	0.28	0.26	0.26	0.26	0.33	0.27	0.26	0.06	0.16	0.05	3
Decapoda	0.25	0.25	0.26	0.29	0.29	0.27	0.24	0.31	0.29	0.24	0.28	0.29	0.30	0.33	12
Euphausiacea	0.27	0.26	0.28	0.26	0.26	0.28	0.21	0.14	0.17	0.24	0.28	0.18	0.18	0.31	6
Chaetognatha	0.28	0.27	0.30	0.28	0.28	0.27	0.24	0.11	0.27	0.24	0.25	−.26	0.31	0.32	9
Crustacea larvae	0.25	0.06	0.30	0.27	0.22	0.25	0.24	0.17	−.09	0.25	0.31	−.25	0.29	0.11	8
Heteropoda	0.15	0.24	0.14	0.18	0.23	0.16	0.29	0.20	0.07	0.19	0.29	0.19	0.27	0.28	14
Larvacea	0.28	0.27	0.17	0.13	0.24	0.27	0.29	0.21	−.05	0.22	−.08	0.29	0.22	0.23	11
Ostracoda	0.22	0.26	−.01	0.26	0.23	0.12	0.18	0.23	0.13	0.18	0.11	−.21	0.21	0.24	16
Cladocera	0.12	0.19	−.03	0.01	0.03	−.23	0.03	−.25	0.06	0.23	0.17	0.11	0.09	−.08	10
Pteropoda	0.19	0.13	0.10	0.08	−.02	0.04	0.12	−.02	−.19	−.06	0.05	−.08	−.17	0.21	15
Mysidacea	0.15	0.17	−.28	0.09	−.15	0.08	0.11	−.12	−.27	0.26	0.14	−.33	0.29	0.16	13

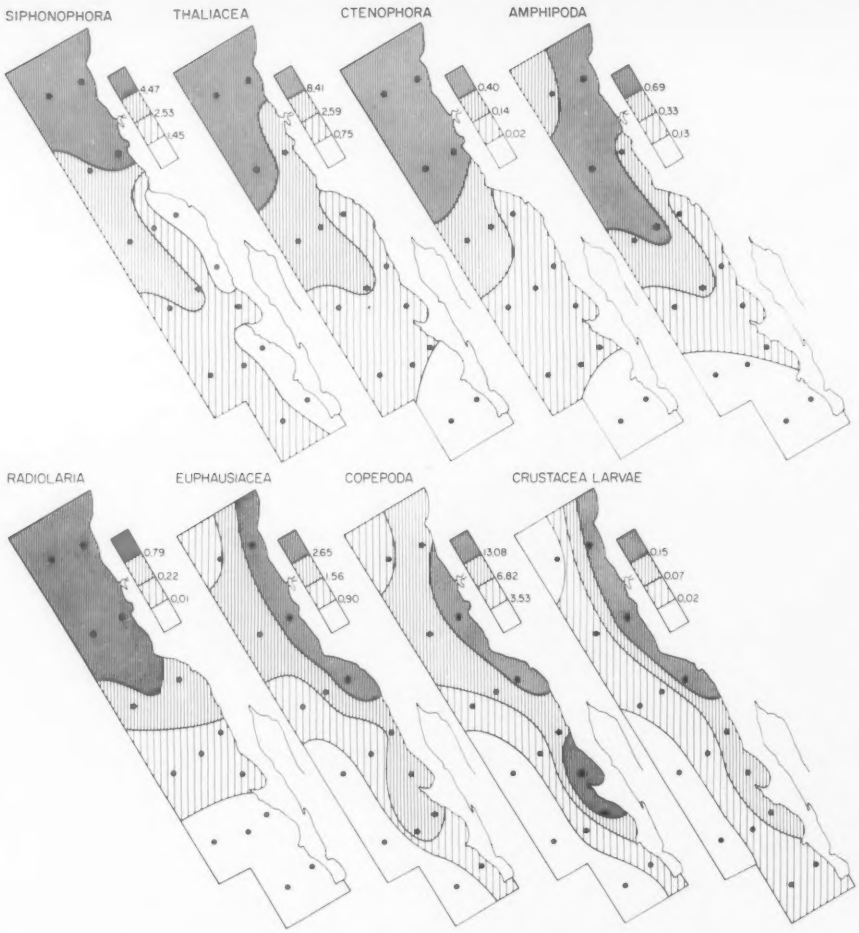


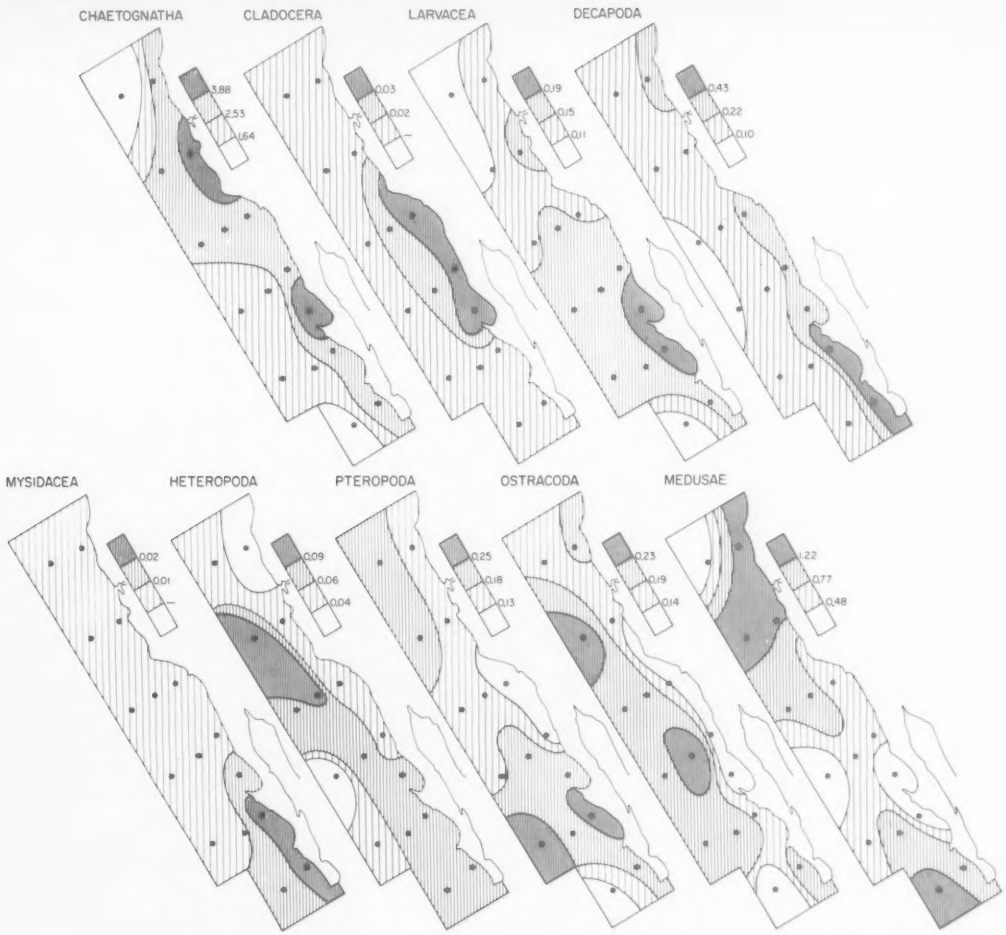
FIGURE 4.—Charts of the geographical distribution of biomass for each of the taxa based on logarithmic means for each standard zone (see Figure 1) for all the CalCOFI cruises for 1955-59. Contours are drawn at levels correspond-

The ranks are given in Table 4, and the value of Spearman's rank correlation coefficient between the two ranks is +0.806 which is significant at the 0.1% level.

Figure 6 shows graphs of the first principal components of the analyses for each taxonomic category with the categories ranked in the same order as in Table 4. All the northern and inshore categories, down to Crustacea larvae in Figure 2, show the same form of year-to-year fluctuations in biomass as do the zones, with relatively high biomass in 1955 and 1956 and low biomass in 1958 and 1959. The remaining categories show some features of this pattern with only Cladocera showing a negative relationship.

These results suggest that whatever influence or influences are responsible for the fluctuations in the plankton either have their origin in the north of the survey area or have a greater effect on those categories with northern patterns of distribution. It is, at least, fairly safe to infer that there is some commonality between the influences which determine geographical distribution and those which are responsible for the form of the year-to-year changes in biomass.

The years from 1955 to 1959 were deliberately



ing to the mean + 1 SD, the mean, and the mean − 1 SD. The keys to the contour levels for each category give the arithmetic values, as grams per 1,000 m^3, corresponding to these levels.

chosen for the production of biomass data to cover a period of marked change in physical conditions and in the distribution of many species in the CalCOFI area. The main features of these changes have been described in the proceedings of a special symposium (Sette and Isaacs 1960). The most striking feature was a considerable warming of the surface waters which started in the south in 1956 and spread through the area during 1957 (see, e.g., Longhurst 1967).

The general form of the change can be typified by the variation in temperature in the top 50 m in the southern California offshore area shown in Figure 7. Favorite and McLain (1973) showed that this is part of a widespread change in surface temperature affecting almost the whole of the North Pacific Ocean. The reasons for the change are not yet completely clear. The initial warming in 1957 appears to be associated with a reduction in the flow of the California Current which occurred between the late summer of 1957 and midsummer 1958. As an index of the flow of the California Current, Saur (1972) used the difference in sea level between Honolulu and San Francisco. A plot of monthly means (with a linear trend removed and adjusted to normal atmo-

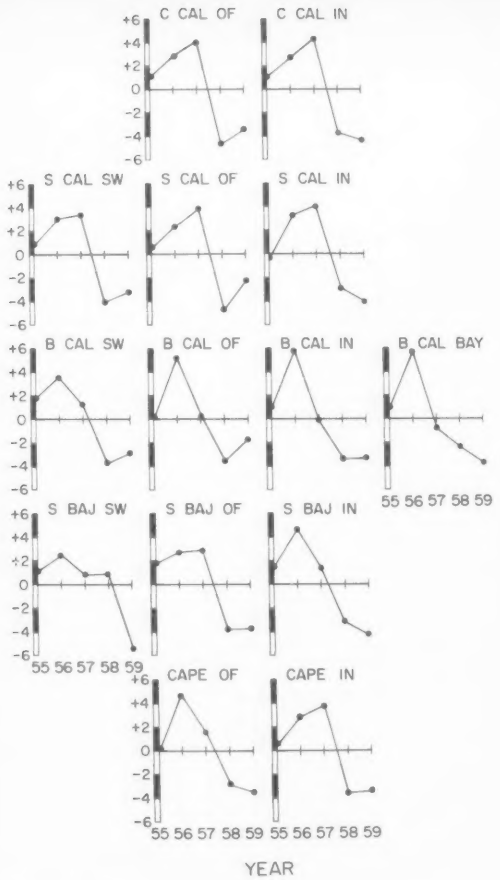


FIGURE 5.—Graphs for each of the well-sampled CalCOFI zones (see Figure 1) of the first principal component of the year-to-year fluctuations in biomass of all the 17 taxa. Each graph is drawn with a mean of zero and the vertical scale is in SD units.

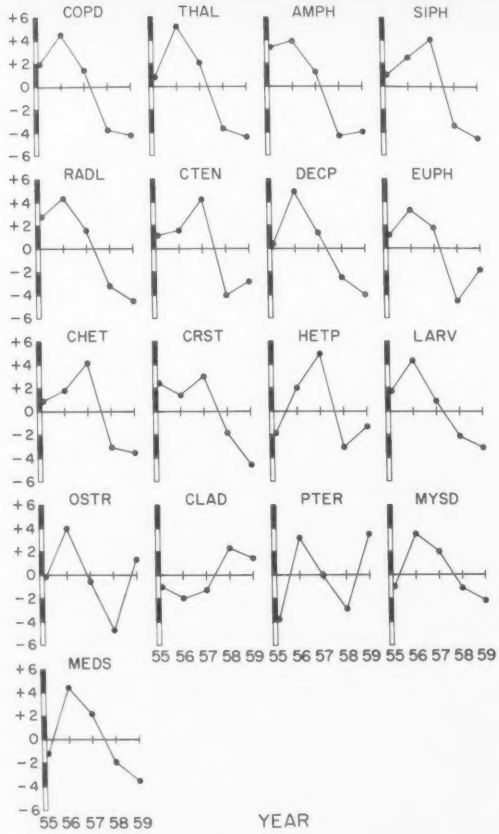


FIGURE 6.—Graphs for each taxon of the first principal component of the year-to-year fluctuations in biomass for all the well-sampled CalCOFI standard zones. A key to the abbreviations of the names of the taxa is given in Table 1. They are in the same order as in Table 4 (see text). Each graph has a mean of zero and the vertical scale is in SD units.

spheric pressure) for 1955-59 is shown in Figure 7. Differences greater than 58 cm are believed to indicate a stronger than normal flow and differences less than 58 cm a less than normal flow. It can be seen that the period of less than normal flow in 1957-58 corresponds well with the timing of the increase in temperature in the southern California offshore zone. In the California Current region, and indeed over most of the eastern North Pacific, the increase in temperature persisted through 1958 and 1959 while the sea level differences indicate a normal or above average flow during this time. The period of below normal flow corresponds with El Niño off the coast of Peru and perhaps with an anomalous weakening of the trade winds of the southern hemisphere and a concurrent reduction of equatorial upwelling (Bjerknes 1966; Favorite and McLain 1973).

Wickett (1967) found a relationship between the year-to-year changes in zooplankton volume for the CalCOFI survey (Thrailkill 1963) and the mean meridional Ekman transport (Fofonoff 1962) for January to August in the previous year at lat. 50°N, long. 140°W (over 1,000 miles upstream from the CalCOFI survey area) for the years 1952-59. He suggested that a major cause of variation in the abundance of zooplankton in the California Current region is the change in the

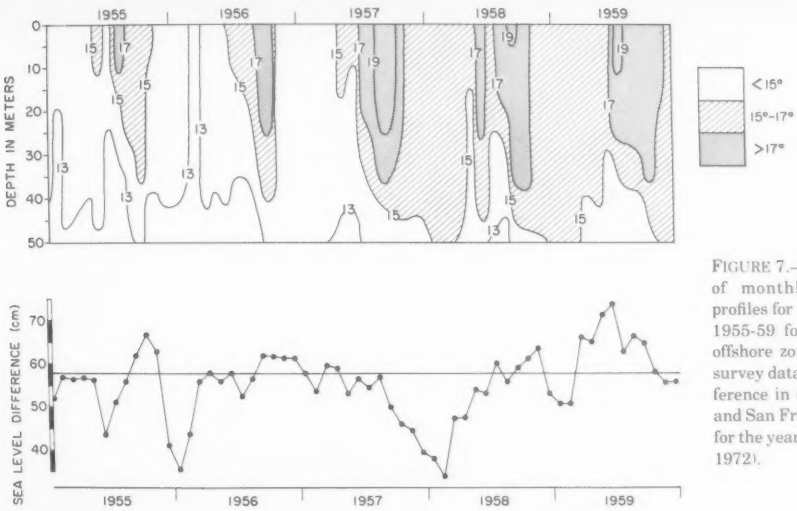


FIGURE 7.—Top) A contoured diagram of monthly vertical temperature profiles for the upper 50 m for the years 1955-59 for the southern California offshore zone (see Figure 1). CalCOFI survey data. Bottom) A graph of the difference in sea level between Honolulu and San Francisco at monthly intervals for the years 1955-59 (plotted from Saur 1972).

proportion of the superficial wind-driven water that is swept southward out of the North Pacific subarctic circulation.

There seems little doubt that the change in temperature in 1957 and its persistence through 1958 and 1959 is related to the relative reduction in biomass of the zooplankton associated with the first principal components of all zones and most of the taxonomic categories. The data presented by Wickett showed a marked reduction in southward transport at lat. 50°N, long. 140°W during 1958 and 1959 and this, coupled with the reduction in the flow of the California Current in 1957 and 1958 (Figure 7), would appear to support Wickett's suggestion of a direct influence by water movements. The relationship between the north to south geographical gradient (Figure 3) and the first principal components is also entirely consistent with this hypothesis.

An examination of the remaining components for each of the zones indicated the existence of a second pattern of fluctuation common to most of the zones. In Figure 8 are given graphs of a component, other than the first, for each zone selected to give the best approximation to a form common to all the zones. In 8 of the 14 zones it is the second component; in the remaining zones it is either the third or the fourth component. Given the quantity and the quality of the original data and considering the large proportion of the variability of the data associated with the first components, the lack of consistency in the position of the common pattern among the components is perhaps not surprising. Figure 9 shows the same for each taxonomic category; again the majority are second components and only one, for Radiolaria, is the fourth component. The main features of the pattern are a low in 1957 and highs in 1956 and 1958; 1955 and 1959 tend to be low but their positions vary somewhat within both the zones and the taxonomic categories.

Coastal upwelling is a feature of the California Current region, and Bakun (1973) has produced estimates of relative fluctuations in upwelling at a number of positions along the west coast of North America. They are based on estimates of the offshore component of the Ekman transport which is in turn estimated from atmospheric pressure fields.

Monthly means of the upwelling index for five positions off the coast at latitude and longitude 36°N, 122°W; 33°N, 119°W; 30°N, 116°W; 27°N, 116°W; and 24°N, 113°W, for the period 1955-58 were extracted from Bakun's report. Uncertainties about the differences in absolute terms between the estimates at different positions particularly off southern California, discussed by Bakun, suggested that principal components might provide a good method of summarizing the data from this set of positions. For each calendar month, analyses were carried out on the index estimates for the five positions and the 5 yr. Examination of the components showed that a pattern common to the first 7 mo of the year was

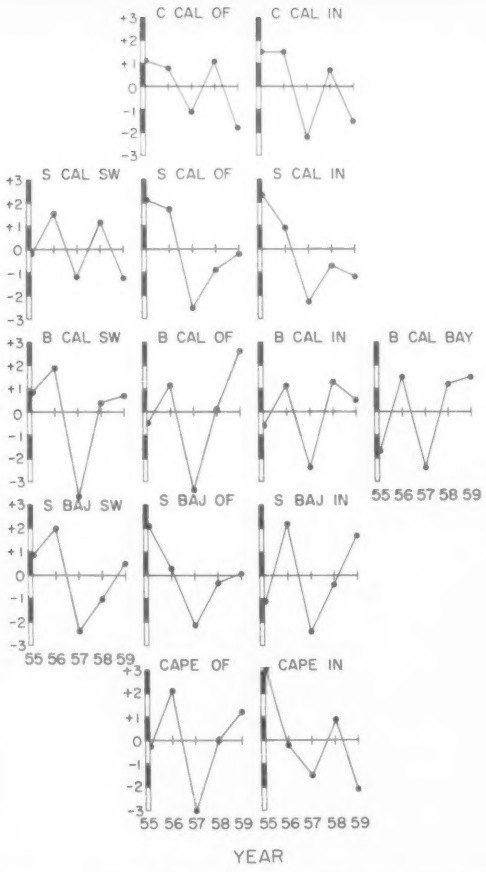


FIGURE 8.—Graphs, for each CalCOFI standard zone, of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 6.

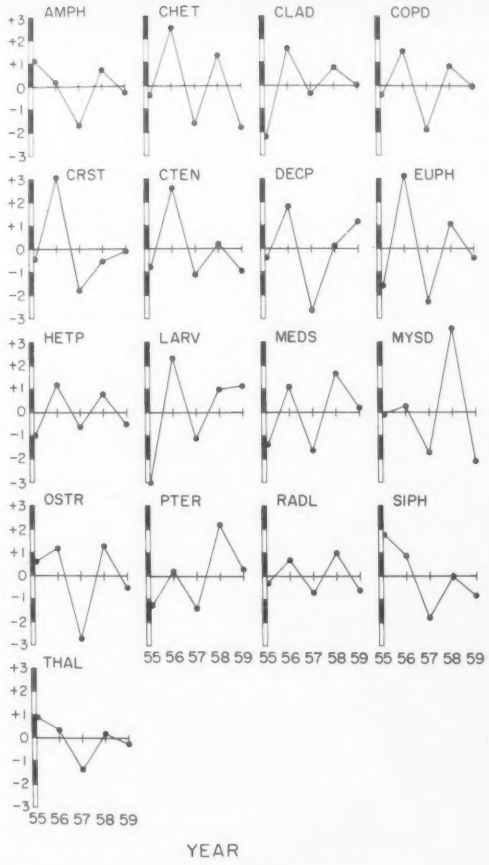


FIGURE 9.—Graphs, for each taxonomic group (Table 1), of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 7.

present within the components, and graphs of these are given in Figure 10. The pattern was found as the first component in all the months except March and April where it was found in the second component. Graphs of the first components for August to December are also given in Figure 10.

There is a marked similarity between the pattern of year-to-year fluctuations in upwelling as represented by the components for the first 7 mo of each year and the fluctuations in biomass of the zooplankton represented by the components shown in Figures 8 and 9, and it is reasonable to assume that some form of causal relationship is involved. As with the first component in relation to the temperature range, the precise mechanisms involved cannot be inferred from the information here. Upwelling has effects on the vertical temperature structure and particularly on the timing of the establishment of a clear thermocline. It can also be expected to have a considerable influence on the supply of nutrients. It is probable, therefore, that the effect on the zooplankton is an indirect one through the influence of vertical stability of the water column and the supply of nutrients on primary production processes. Peterson (1973) has established a relationship between year-to-year variation in upwelling

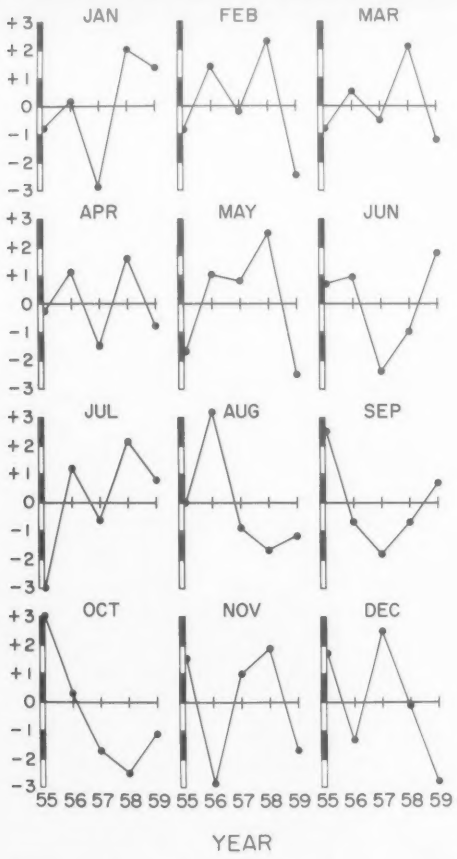


FIGURE 10.—Graphs of principal components of upwelling index for the CalCOFI survey area for each month for the years 1955-59. See text and Bakun (1973).

off the coast of Oregon and the catch of the Dungeness crab, *Cancer magister*, with a time lag of about 18 mo. He attributed this to an increased food supply in years with pronounced upwelling, implying a relationship between upwelling and plankton similar in sign to that found further south in the California Current.

CONCLUSIONS

At least during the period 1955-59, a considerable proportion of the variability from year to year in the biomass of zooplankton, as represented by estimates for the taxa listed in Table 1, can be associated with hydrographic events, variations in the strength of the California Current, and variations in the intensity of coastal upwelling. The precise mechanisms involved are not clear, but in relation to the California Current there is a similarity in the relationships within the taxa with respect to both geographical distribution and annual fluctuations in abundance which suggests that advection of stocks may be involved to a considerable extent. The influence of upwelling on primary production through effects on temperature stratification and the supply of nutrients probably accounts for the relationship with the zooplankton.

The only data that have been produced routinely from the whole series of CalCOFI cruises, which relate to plankton other than fish eggs and larvae, are in the form of displacement volumes of unsorted samples (Smith 1971). The marked coherence between the various taxonomic categories suggests that these data can be expected to produce estimates of long-term variations which indicate real changes in the abundance of the zooplankton. Such data cannot, however, reflect the geographical differentiation within the zooplankton, and this imposes a limit, to the extent to which they can be used, to provide the basis for the examination of the influences of a complex of environmental factors of the kind suggested by this study as playing an important role in determining the year-to-year fluctuations in the plankton.

The taxonomic categories used in this study were selected by Isaacs et al. (1969) to represent the plankton as food for fish. I have used them to represent fluctuations in the zooplankton as such for the 1955-59 period.

For future studies the only definitive method of selecting taxa to represent year-to-year changes in the zooplankton is by trial and error: there are, moreover, numerous possibilities, and the labor involved would be prohibitive if some compromise is not made. It is indicated above that there is a tendency for taxa which have similar geographical distributions also to show similar year-to-year fluctuations in abundance. As a first approximation, this fact might be used as a guide to the selection of representative categories. It is implicit that each selected category should be geographically homogeneous, and the set of categories should cover the full range of geographical distributions.

It is probable that the species is the highest taxon for which geographical homogeneity can be assumed, and even here there may be some species which have geographically differentiated races. Isaacs et al. (1969) gave an estimate of about 550

species found, or likely to be found, in the zooplankton of the CalCOFI survey area. Allowing for the fact that somewhere between one-half and three-quarters of these species will probably occur infrequently in samples, the labor involved in routinely analyzing for this number of species is very considerable. The geographical distributions of species belonging to many of the major taxa within the zooplankton have been studied and published in the CalCOFI Atlas series which could provide the basis for the selection of a limited number of species which will represent the range of geographical distributions in the survey area and, hopefully, will provide a good representation of the range of year-to-year fluctuations in abundance.

ACKNOWLEDGMENTS

My thanks are due to Brian Rothschild, Director, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for making available to me the facilities of the La Jolla Laboratory. I also thank J. D. Isaacs for furnishing unpublished data. Nancy Wiley and Dorothy Roll were of great assistance in the computations involved in the study and John G. Wyllie helped with some data problems. Finally I must thank Paul E. Smith whose knowledge of the California Current region and of the CalCOFI survey was invaluable. My visit to the La Jolla Laboratory was supported by the U.K. Natural Environment Research Council.

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POPULATION BIOLOGY OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, STOCKS IN THE WASHINGTON-QUEEN CHARLOTTE SOUND REGION, AND THEIR RESPONSE TO FISHING[1]

DONALD R. GUNDERSON[2]

ABSTRACT

Production and catch per unit effort of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region have declined drastically in recent years, largely as a result of Soviet and Japanese exploitation during 1966-69. In the region off Washington and southern Vancouver Island, production declined from 39,000 metric tons in 1967 to 6,000 metric tons in 1969, and catch per hour declined 45% during the same period. Pacific ocean perch are ovoviviparous, and so their populations lack the resilience of highly fecund, oviparous groups such as the gadoids. Their ability to maintain even current levels of abundance is uncertain.

Age composition, growth rates, and mortality rates were estimated for two separate stocks occupying this region: one in Queen Charlotte Sound, B.C., and one occupying the area off northern Washington and southern Vancouver Island. Instantaneous rate of natural mortality was estimated to lie between 0.1 and 0.2. Recruitment to the fishing grounds is not complete until age 16 and the proportion of each age group vulnerable to fishing was estimated by stock for age groups 10 (0.31-0.35) through 15 (0.87-0.94).

Age at sexual maturity ($t_{0.50}$) differed between stocks, ranging from 9 to 11 yr for females and 6 to 7 yr for males. Fecundity was determined for several females, and the fecundity-length and fecundity-age relationships discussed. For a variety of reasons, all fecundity estimates were regarded as tentative, bearing a rather uncertain relationship to the number of larvae released.

The effects of fishing on stocks of Pacific ocean perch were examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment, although the computer program developed for this study enabled estimation of exploitable biomass and population fecundity as well as yield per recruit.

Compensatory mechanisms that would tend to restore population fecundity and recruitment to preexploitation levels were discussed, and the limits of some of these mechanisms (density dependent growth and earlier sexual maturation) were explored with the computer program mentioned previously. The results of this analysis suggested that past levels of exploitation went far beyond those levels that could be sustained by Pacific ocean perch stocks on a long-term basis. It was coucluded that future rates of exploitation should be regulated so that the annual catch never exceeds 10% of the mean stock biomass on hand during the year.

Pacific ocean perch, *Sebastes alutus* (Gilbert), are found throughout the northern Pacific, from California to the Bering Sea, and as far southwest as the Kurile Islands. Murphy (1968) has shown that species with several reproductive age-groups are well adapted to unpredictable levels of larval mortality, and Pacific ocean perch seem to be a prime example of this line of evolution. Twenty-year-olds are common in this species, and there are 10 or more reproductive age-groups of significance. In the unexploited state, large standing stocks of *S. alutus* accumulated, furnishing a substantial hedge against uncertain larval survival. Quast (1972) estimated the original catchable biomass of *S. alutus* off western North America to be roughly 1,750,000 metric tons.

Commercial fishing for *S. alutus* was initiated in 1946 by U.S. trawlers operating off central Oregon (Alverson and Westrheim 1961). Development proceeded slowly, but by 1955, United States and Canadian vessels were harvesting *S. alutus* from as far north as Queen Charlotte Sound, B.C. Westrheim et al. (1972) have characterized the North American trawl fishery for Pacific ocean perch as undergoing a short development period (1946-51) with low production, a longer period (1953-60) of moderate production, and a short period (1961-66) of increasing production. Since

[1]Based on a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree, University of Washington.

[2]Washington State Department of Fisheries, Fisheries Center, University of Washington, Seattle; present address: Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

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1966, Pacific ocean perch production has fallen drastically in several areas fished by these North American trawlers, largely because of excessive catches by Japanese and Soviet fleets.

Japanese and Soviet trawl fisheries for Pacific ocean perch began in the Bering Sea about 1960 and expanded southward into the eastern Gulf of Alaska in 1963. The Soviet fleet operated throughout the Queen Charlotte Sound-Oregon region by 1965, and they were joined by Japanese trawlers in 1966. Catches from the Oregon-Queen Charlotte Sound region were quite high initially (Figures 1 through 3), but the stocks were far too limited to sustain these harvests. By 1969, *S. alutus* stocks were severely depleted throughout the Oregon-Vancouver Island region (Figures 1, 2). Production in the International North Pacific Fisheries Commission (INPFC) Vancouver and Columbia areas plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period (Westrheim et al. 1972). Data on catch per unit effort (CPUE) suggest that the exploitable biomass of Pacific ocean perch in the Vancouver-Columbia region has changed little since 1969, despite the fact that a series of relatively strong year classes have recruited to the fishery.

Pacific ocean perch stocks in Queen Charlotte Sound were affected less drastically by fishing than those in the Oregon-Vancouver Island region. Biomass estimates and CPUE data (Westrheim et al. 1972) indicated that *S. alutus* were initially more abundant in the former area and that they did not undergo such intensive exploitation. During 1966-68, production declined 50% while CPUE of Washington trawlers declined 36%. Fishing effort was reduced substantially after March 1971, when most of Queen Charlotte Sound was declared to be an exclusive Canadian fishing zone. Bilateral agreements between Canada and the United States allowed the traditional United States fishery for *S. alutus* to continue, but Japanese and Soviet fishing was prohibited. Recent information, however, indicates that in 1974, large catches of Queen Charlotte Sound Pacific ocean perch were made by Japanese vessels

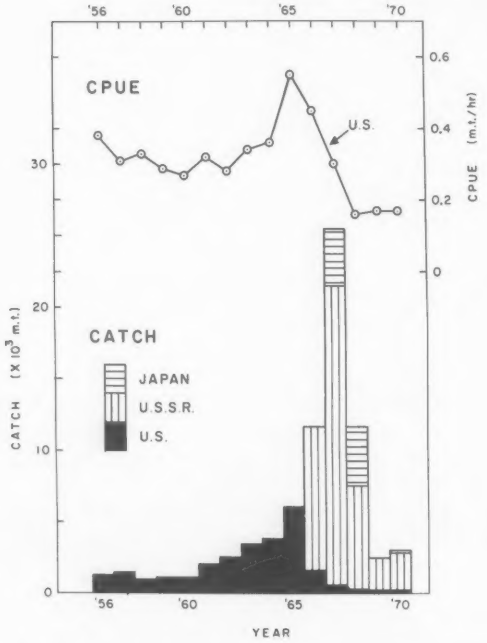

FIGURE 1.—Catch and CPUE data for Pacific ocean perch in the INPFC Columbia area (from Westrheim et al. 1972).

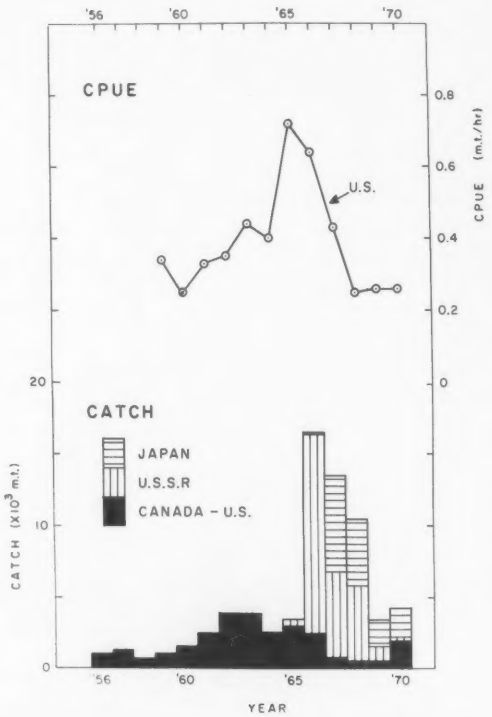

FIGURE 2.—Catch and CPUE data for Pacific ocean perch in the INPFC Vancouver Area (from Westrheim et al. 1972).

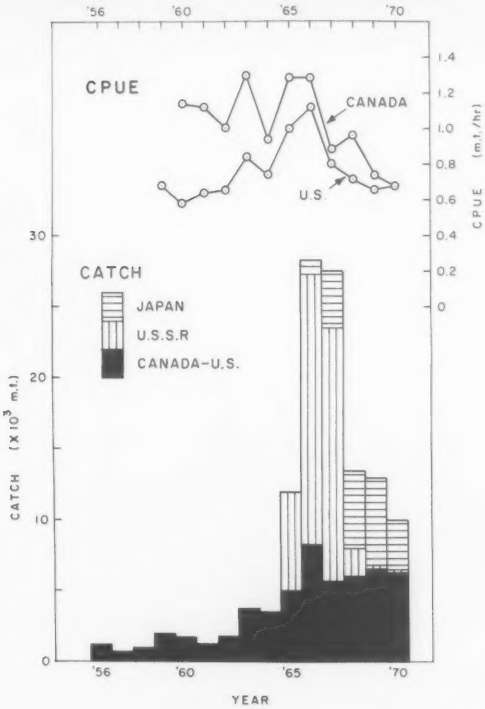

FIGURE 3.—Catch and CPUE data for Pacific ocean perch in Queen Charlotte Sound (from Westrheim et al. 1972).

operating outside the Canadian fishing zone (Gunderson et al. 1977).

Both biomass and longevity have been drastically reduced for Pacific ocean perch throughout the Washington-Queen Charlotte Sound region, and it seems unlikely that the current situation will be stable over the long term. The purpose of this study is to outline the population biology of *S. alutus* stocks in the Washington-Queen Charlotte Sound area and to examine their immediate and long-term response to different harvesting strategies.

METHODS AND MATERIALS

Delineation of Stocks

Two stocks of *S. alutus* will be examined and contrasted: one in Queen Charlotte Sound (QCS) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI).

The QCS stock is contained wholly within Queen Charlotte Sound. North of lat. 52°N, the continental shelf off western Graham Island is quite narrow and there is little available habitat for *S. alutus*. Recent work by Westrheim[3] has shown that previously unexploited stocks exist in Moresby Gully, an undersea canyon extending into Hecate Strait, north of lat. 52°N. The Triangle Islands form a definite southern limit for this stock, since Pacific ocean perch catches immediately south of these islands are almost negligible. Pacific Marine Fisheries Commission (PMFC) statistical areas 5A and 5B offer a convenient unit for studying this stock.

The northern limit of the WVI stock lies somewhere near the middle of Vancouver Island and, for practical reasons, this was represented by the northern boundary of PMFC area 3C (lat. 49°N). Pacific ocean perch catches in PMFC area 3D have been quite limited historically (Figure 4), and during 1966-72, only 13% of the Washington landings in the INPFC Vancouver area came from there (Table 1).

The southern limit of the WVI stock is more difficult to establish. Since Pacific ocean perch catches by Washington trawlers fall off sharply south of PMFC area 3B-3C (lat. 47°20'N), this was the boundary used throughout this study. This boundary, as well as the others used in this report, is in basic agreement with Snytko (1971), whose

[3]Westrheim, S. J. 1974 Echo-sounder and trawl survey of Queen Charlotte Sound and southern Hecate Strait, 1971-73. Fish. Res. Board Can. Manuscr. Rep. 1307, 43 p.

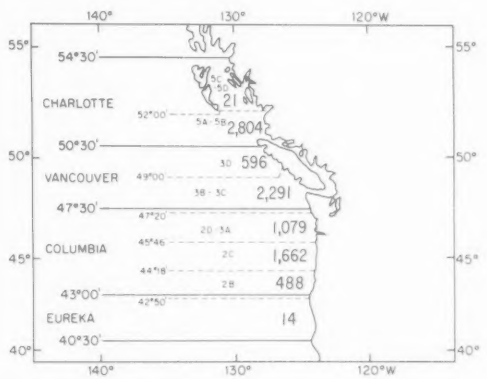

FIGURE 4.—Chart of the northeastern Pacific Ocean showing INPFC and PMFC statistical areas used in this study. Mean annual Pacific ocean perch catch (metric tons) during 1960-65 (heavy lettering) is shown for each PMFC Area.

TABLE 1.—Catches (in metric tons) of Pacific ocean perch by different components of the international trawl fleet, 1966-72.

	Washington			United States and Canada		All nations	
Year	3B-3C	3B-3D	5A-5B	3B-3D	5A-5B	3B-3D	5A-5B
1966	2,104	2,283	5,616	2,358	8,252	16,358	27,054
1967	701	783	5,341	805	5,745	17,746	26,741
1968	459	526	4,787	552	6,051	9,905	13,492
1969	462	573	4,992	583	6,628	4,513	12,951
1970	980	1,208	4,308	1,955	6,077	4,955	9,854
1971	638	718	2,925	1,155	4,165	4,138	4,867
1972	419	504	3,364	624	5,561	3,082	7,842
Total	5,763	6,595	31,333	8,032	42,479	60,697	102,801

research cruise data suggested that the two most significant aggregations of *S. alutus* in the Vancouver-Oregon region were found at lat. 48°-50°N and lat. 46°-47°N. For all practical purposes then, PMFC Statistical areas 3B and 3C offer a convenient unit for studying the WVI stock.

Data Employed

Production records used in this study came from the Washington State Department of Fisheries, PMFC, INPFC, and from data furnished during U.S.-U.S.S.R. scientific meetings.

Landings by Washington trawlers made up a relatively small proportion of the total international landings during the 1966-72 study period, but the quality of their production records is such that the CPUE data from this fleet offer the best available index of stock abundance. During 1966-72, the Washington landings made up 30% of the total international catch from Queen Charlotte Sound, and 11% of the catch from the INPFC Vancouver area (Table 1). Washington trawlers accounted for the bulk of the North American landings in these areas, however, landing 74% of the Pacific ocean perch caught in Queen Charlotte Sound and 82% of those from the INPFC Vancouver area during 1966-72.

Most of the data on age composition (as determined from otoliths), length composition, and maturity were obtained by sampling the catches landed by Washington trawlers and were collected during 1967-72. Data from research vessel cruises off Washington and Oregon were used to estimate growth rates and fecundity-length relationships for the WVI stock.

MIGRATIONS AND AVAILABILITY

General Features of the Life History

Extensive investigations into the life history of *S. alutus* have been carried out in the Bering Sea (Paraketsov 1963; Pautov 1972; Chikuni 1975), Gulf of Alaska (Lyubimova 1963, 1964, 1965; Fadeev 1968; Chikuni 1975), and in the Queen Charlotte Sound-Oregon region (Alverson and Westrheim 1961; Westrheim 1970, 1973, 1975; Gunderson 1971, 1974; Snytko 1971). These studies have shown that there are several basic similarities in the life history and biology of Pacific ocean perch throughout its range.

Age and growth analyses have shown that *S. alutus* attain sexual maturity relatively late in life (6-10 yr), grow slowly, and are long-lived. In lightly fished stocks, *S. alutus* may reach an age of 30 yr (Alverson and Westrheim 1961; Paraketsov 1963).

Sebastes alutus is an ovoviviparous species, with three distinct phases in its reproductive cycle. These are: mating (when spermatozoa are transferred from males to females), fertilization (when the ova are actually fertilized), and spawning (when the larvae are released).

Well-defined bathymetric migrations occur in all areas. Pacific ocean perch occupy relatively shallow water during the summer feeding period, then move to deep water during winter. The depths inhabited seem to vary little throughout the geographic range, despite significant differences in thermal conditions (Table 2). Mating occurs shortly before or during migration from shallow water, but fertilization and embryo release do not occur until the fish are in deep water.

The larvae of *S. alutus* are pelagic and do not settle into a demersal existence until 2-3 yr old. Juveniles and young adults are confined to the shallowest portions of the adult bathymetric range, so that size and age composition vary widely at different depths.

Despite these common characteristics, there are substantial geographic differences in life history and migration patterns, even within the relatively restricted region dealt with in this study. For this reason, migration patterns, seasonal availability, age composition, growth, age at maturity, and

TABLE 2.—Depth and temperature characteristics of Pacific ocean perch habitat.

	Depths of maximum abundance (m)		Temperature (°C)	
Area	Summer	Winter	Range	Optimum
Vancouver-Oregon (Snytko 1971)	200-300	350-450	4.0-9.5	6-8
Gulf of Alaska (Lyubimova 1965)	180-250	250-420	2.5-6.5	3-5
Bering Sea (Pautov 1972)	150-350	350-450	1.0-6.0	3-4

fecundity must be discussed separately for the QCS and WVI stocks.

Migrations and Availability Within the Study Area

Availability of *S. alutus* fluctuates widely over short periods of time. Short-term fluctuations in availability were quite evident during a series of 2- to 3-wk research cruises off the Washington coast (Gunderson 1974), and masked any long-term changes in biomass that occurred during 1968-72.

For this reason, catch and CPUE data can be used to study migration patterns and seasonal availability only if they are based on a large quantity of trawling effort, carried out more or less continuously. The data from the Washington trawl fleet seem well suited to this purpose, since these trawlers spend a great deal of time searching out and catching Pacific ocean perch. *Sebastes alutus* is frequently the target species for this fleet, and made up 29% of its total coastal landings during 1967-71.

In this section, catch and effort data from the Washington trawl fleet will be used to describe migration patterns and seasonal trends in the availability of *S. alutus*. Data on sex and length composition of the catch will also be brought into the analysis, since it is difficult to interpret trends in availability without them.

Queen Charlotte Sound

Seasonal Patterns for the Region

The continental shelf is steep and untrawlable seaward of 150 fm (274 m) in Queen Charlotte Sound, so the fish in this area are inaccessible to trawlers when they move into deep water (January-April). Examination of gonads indicates that spawning occurs in March (Gunderson 1971), but there is no certainty as to where this occurs. Few fish are caught during January-April, and virtually all of these are males (Figure 5) that do not participate in the spawning migration.

Males precede females in their return from wintering areas, and when the fishery first begins in earnest (May), males constitute 68% of the catch. The availability of females increases sharply after May, and by July they dominate the catches.

During June-August, Pacific ocean perch are at the shallowest point in their bathymetric cycle. Catches are low during this period, and large quantities of fish 35 cm or smaller are landed (Figure 6).

Both catch and CPUE rise in September, and although the mean depth of catch is about the same as in July and August, there is a sharp increase in the proportion of fish larger than 35 cm in the catch. Aggregations of large adults must suddenly become available during September, probably because mating activities are beginning.

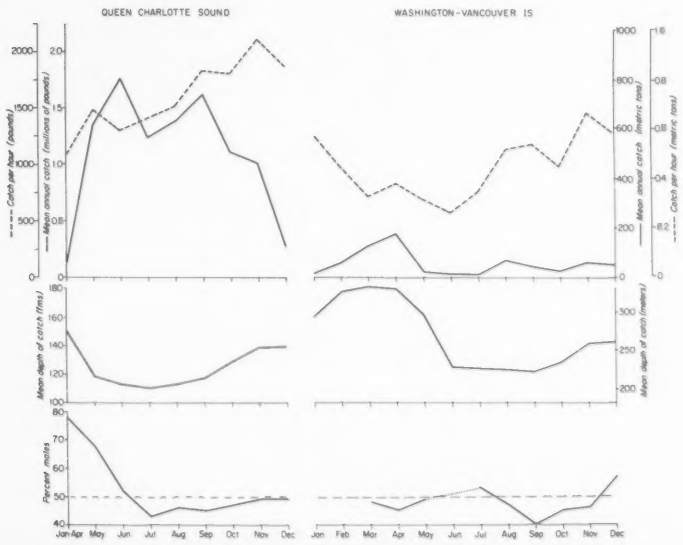
QUEEN CHARLOTTE SOUND
WASHINGTON-VANCOUVER IS
Catch per hour (pounds)
Mean annual catch (millions of pounds)
Mean annual catch (metric tons)
Catch per hour (metric tons)
Mean depth of catch (fms)
Mean depth of catch (meters)
Percent males
Jan-Apr May Jun Jul Aug Sep Oct Nov Dec
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

FIGURE 5.—Mean monthly catch, catch per hour, mean depth of catch, and sex ratio for the Washington trawl fleet during 1967-71. Data for the QCS and WVI stocks of Pacific ocean perch are presented separately.

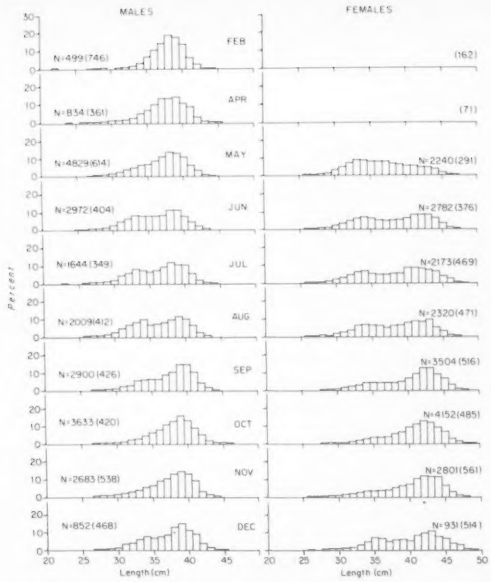

FIGURE 6.—Size composition of 1967-71 Pacific ocean perch catches from Queen Charlotte Sound, by month. Mean numbers caught per hour during 1967-71 are shown in parentheses.

Previous work (Gunderson 1972) has shown that these aggregations are faster growing, but only slightly older, than the rest of the stock.

Pacific ocean perch move into progressively deeper water during October-December, as they return to deepwater spawning areas. Catch per hour remains high during this period, but deteriorating weather conditions force a decline in trawling effort and landings.

Because catch, CPUE, sex ratio, length composition, and age composition all varied with season, the data from different time periods were treated independently in much of the later analysis. The time periods utilized were January-April, May, June-August, and September-December.

Seasonal Patterns for Specific Grounds

The geographic distribution of the catch varied from month to month (Figure 7) and there is a possibility that between-ground variations in size composition could contribute to the results shown in Figure 6. Length and age composition data were analyzed by fishing ground (Figure 8) to examine this point further. To insure that the data used were as typical as possible of the grounds in question, only samples from characteristic fishing depths were chosen for this analysis. The 1967-71 mean depth of catch was computed for each month and ground in question, and only those samples whose range was within 15 fm (27 m) of this mean were analyzed.

The results (Figure 9) show that within a given time period, length composition differed somewhat between grounds, but the differences showed no consistent, predictable pattern. There was no ground that could always be characterized as having larger or smaller fish than the other grounds. Size composition data for SE Corner, SW Corner, and Triangle grounds, the three major fishing grounds, showed only slight between-ground heterogeneity within any given time period.

Washington-Vancouver Island

Unlike Queen Charlotte Sound where the continental shelf drops off abruptly past 150 fm (274 m), a wide range of depths can be fished off Washington and Vancouver Island (Figure 5). Trawlers can follow fish in this area into deepwater spawning areas, and exploit them year around. The year can be divided into a

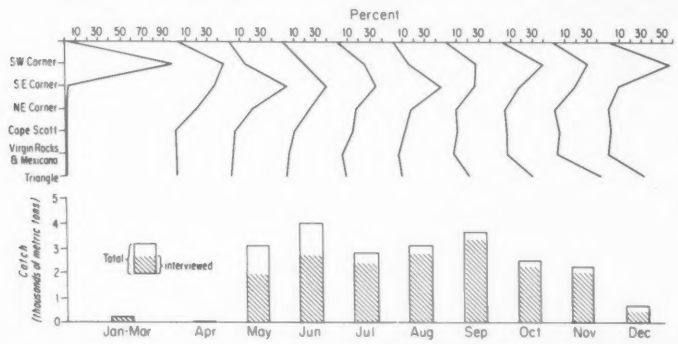

FIGURE 7.—Distribution of 1967-71 Pacific ocean perch catch from Queen Charlotte Sound by month and fishing ground. Data on distribution by ground were derived from the portion of the catch for which fishermen interviews were available. The Virgin Rocks-Mexicana ground includes Virgin Rocks and all grounds east of the Cape Scott ground.

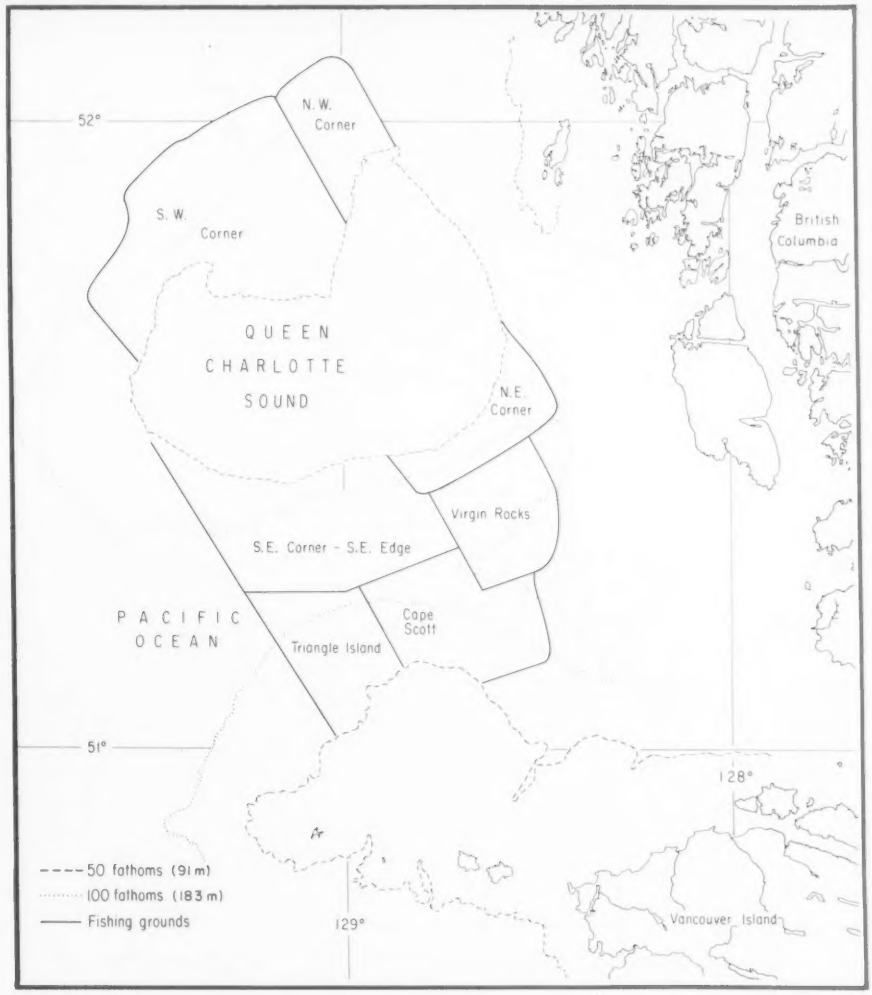

FIGURE 8.—Major Pacific ocean perch fishing grounds in Queen Charlotte Sound, B.C.

November-May period when most of the fish are in deepwater spawning areas, and a June-October period when they are in shallow water. Mean depth of catch is 140-180 fm (256-329 m) during the November-May period, and 120-130 fm (219-238 m) during June-October.

Seasonal variability in the biological composition of the catch is less significant than in Queen Charlotte Sound, since the sex ratio is close to 50% males all year. Data on the size composition of the catch was quite limited during certain months, but size composition generally seemed to depend on the depths at which the fishery was operating. The proportion of small fish (35 cm or smaller) in the landings was highest during the shallow-water fishery, and decreased during November-May (Figure 10).

Considering the wide differences in the magnitude of the landings between Washington-Vancouver Island and Queen Charlotte Sound, CPUE levels are surprisingly similar (Figure 5). Results of research cruises have shown that the availability of Pacific ocean perch varies widely in the Washington-Vancouver Island region (Gun-

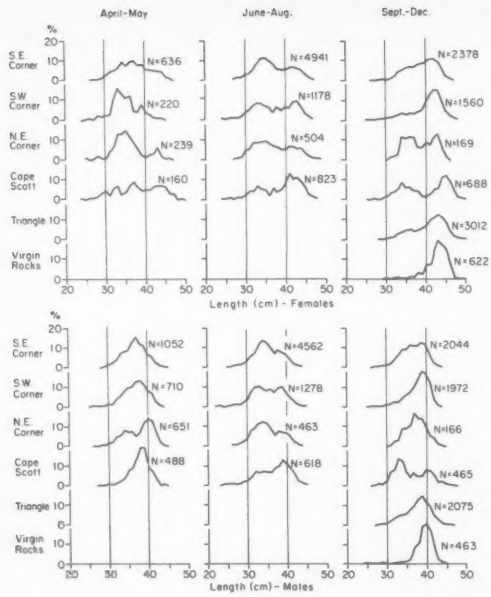

FIGURE 9.—Size composition of 1966-72 Pacific ocean perch catches in Queen Charlotte Sound, by fishing ground and season.

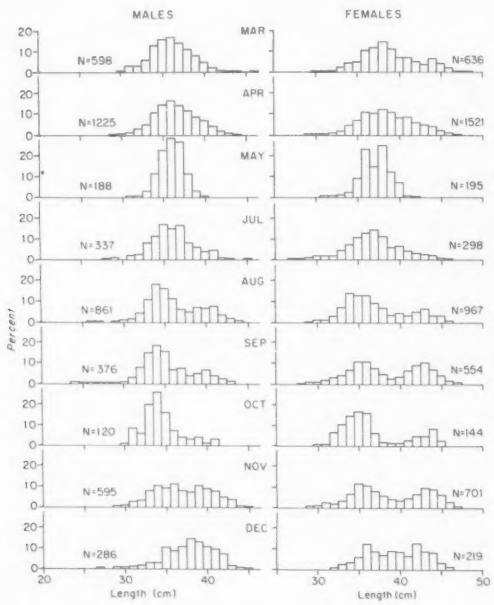

FIGURE 10.—Size composition in 1967-71 Pacific ocean perch catches from Washington-Vancouver Island, by month.

derson 1974), and fishermen probably restrict their efforts to periods of high availability. If this is the case, the relative levels of monthly catch give the best index of stock availability. Peak availability occurs during March-April (near the time of embryo release) and in August-December (near the mating period). This pattern of seasonal availability agrees well with results from previous studies of the WVI stock (Gunderson 1971; Snytko 1971).

AGE-LENGTH RELATIONSHIPS

Queen Charlotte Sound

The age-length relationship in any sample of Pacific ocean perch from Queen Charlotte Sound is influenced by the availability of large, fast-growing fish, the depth at which the fish were captured, and the proportion of the annual growth completed. In order to examine the relative importance of these factors, analysis similar to that outlined by Gunderson (1974) was employed.

This involved fitting observed mean length at age data to the von Bertalanffy growth model,

$$l_t = L_\infty(1 - \exp{-K(t - t_0)})$$

where l_t = length of fish in centimeters at t years
L_∞ = theoretical asymptotic length
K = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $l_t = 0$.

The least squares technique of Tomlinson and Abramson (1961) was employed to do this, and a separate age-length relationship was computed for each combination of fishing ground and season (April-May, June-August, and September-December) where adequate data were available. All comparisons of the age-length relationship at different grounds and seasons could then be made by comparing fitted length at some common age (age 15 in this case).

The results (Figure 11) show that the age-length relation is more dependent on the availability of fast-growing fish to bottom trawls than on any other factor examined. The main line of evidence supporting this is the close correspondence between changes in fitted length at age 15 (Figure 11) and seasonal changes in size composition (Figure 9), a situation that would be expected if both depend on the availability of large, fast-growing

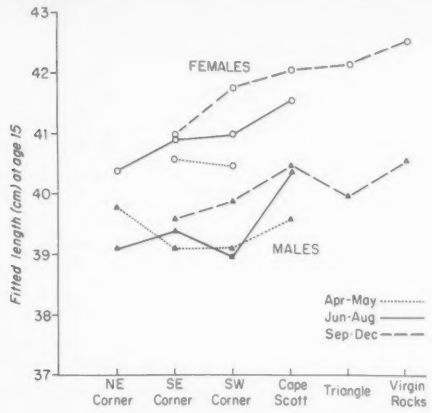

FIGURE 11.—Fitted length at age 15 for Pacific ocean perch in Queen Charlotte Sound (1966-72), by fishing ground, season, and sex.

fish. Both age-length and size composition data indicate that aggregations of these fish are least available during April and May, and that it is only during September-December that they are fully available on all fishing grounds. This general pattern seemed to hold throughout Queen Charlotte Sound, at least on the major fishing grounds. In some instances, however, availability of large, fast-growing fish was unusually high on a relatively minor fishing ground. This seemed to be the case at NE Corner during May and Cape Scott during June-August (Figures 9, 11).

Sampling problems caused by disporportionate fishing intensity in extremes of the bathymetric range are usually insignificant compared with the problems caused by differential availability. Research cruises have shown that mean length at age decreases as depth increases (S. J. Westrheim, pers. commun.), so that fitted length at age 15 should either remain constant (if fishery shifts in response to stock location) or decrease (if fishery shift is independent of stock location) as the fishery shifts to deeper water during September-December (Figure 5). Instead, mean length at age actually increases during September-December (Figure 11) because this is the season when large, fast-growing fish are most available.

Considering all sources of data on catch, CPUE, and biological composition of the landings, it is apparent that there is a significant increase in the size of the exploitable population inhabiting Queen Charlotte Sound during September-December. Age-length data collected during January-August consequently apply to only a fraction of the known population in Queen Charlotte Sound. If it is assumed that all Pacific ocean perch are fully vulnerable to fishing by fall, however, the September-December market sampling data can be taken as representative of the exploitable segment of the QCS stock.

Consequently, 1967-71 age-length data from September-December market samples were used to estimate growth parameters for the QCS stock. Queen Charlotte Sound was treated as a unit, mean length at each age was determined by sex, and the resulting data were fitted to the von Bertalanffy growth model. Both the original data and fitted mean length at age are shown in Table 3.

Washington-Vancouver Island

Availability of Pacific ocean perch in this region influences the age-length relationship, but in a different manner than in Queen Charlotte Sound. Results from research surveys off northern Washington (Gunderson 1974) suggest that mean length at age actually decreases with increasing availability, rather than increasing. The highest rates of catch in this region were obtained when aggregations of large, old, slow-growing fish were most available.

The WVI and QCS stocks also differ substantially in the degree to which mean length at age varies with depth. In contrast to Queen Charlotte Sound, mean length at age has been shown to decrease sharply as depth increases off Washington and Vancouver Island (Westrheim 1973; Gunderson 1974). The decline is so sharp, in fact, that Westrheim (1973) has suggested that there are separate shallow and deepwater stocks in this region.

It is clear, then, that both depth of fishing and availability must be taken into consideration in order to arrive at an age-length relationship that characterizes the WVI stock. Research cruise data obtained off the coast of northern Washington (Gunderson 1974) are particularly well suited to do this, since age-length relationships and availability were systematically observed throughout the bathymetric range. Availability varied widely during these cruises, and, as previously mentioned, this phenomenon masked any long-term changes that occurred during 1968-72. Availability was maximal during the July 1972 cruise, however, and the results from that cruise were used to represent growth in the WVI stock.

TABLE 3.—Number of age-leng'h observations, mean length (centimeters), and fitted length at each age for QCS and WVI stocks of Pacific Ocean perch.

	QCS stock						WVI stock					
	Males			Females			Males			Females		
Age	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length
2							3	18.0	18.1	2	18.5	19.1
3							1	22.0	21.2	1	22.0	21.6
4							10	23.7	23.9	11	24.5	24.0
5	8	27.0	26.6	4	26.2	26.0	18	25.8	26.3	6	26.5	26.1
6	19	29.1	28.6	26	29.4	28.4	9	28.3	28.4	10	28.1	28.0
7	70	30.0	30.5	73	30.6	30.6	8	29.6	30.2	5	28.5	29.8
8	164	31.6	32.2	124	32.1	32.6	34	32.3	31.8	21	31.4	31.4
9	186	33.1	33.6	173	33.5	34.3	58	33.2	33.2	22	33.2	32.9
10	219	34.4	35.0	213	34.8	35.9	123	34.2	34.4	71	34.6	34.3
11	233	36.1	36.1	179	36.3	37.2	172	35.5	35.5	123	35.7	35.5
12	411	37.4	37.1	253	38.3	38.5	78	36.3	36.5	89	36.5	36.6
13	463	38.5	38.0	374	40.0	39.6	42	37.0	37.3	72	37.6	37.6
14	417	39.4	38.9	459	41.2	40.6	59	38.0	38.0	57	38.0	38.6
15	308	40.1	39.6	468	42.2	41.4	56	38.9	38.6	58	39.0	39.4
16	203	40.5	40.2	377	43.2	42.2	50	39.7	39.2	61	40.8	40.2
17	116	41.1	40.8	308	43.6	42.9	37	40.2	39.7	75	41.3	41.0
18	80	41.1	41.3	186	44.0	43.6	24	40.8	40.1	52	41.7	41.6
19	30	41.6	41.7	115	44.4	44.1	29	41.1	40.5	36	42.2	42.2
20	14	41.9	42.1	92	44.2	44.6	16	41.3	40.8	30	42.4	42.7
21	13	41.9	42.5	36	45.1	45.0	7	41.4	41.1	14	43.7	43.2
22				10	45.0	45.4	2	39.0	41.4	16	43.6	43.7
23				3	45.3	45.8				7	43.9	44.1
24				7	45.6	46.1				4	44.5	44.5
	von Bertalanffy growth function parameters											
L_∞	45.25			48.75			43.15			48.47		
K	0.1192			0.1135			0.1320			0.0908		
t_0	−2.4157			−1.7159			−2.1186			−3.5041		
SE of estimate	0.44			0.64			0.68			0.45		

Data from the 120-, 160-, and 200-fm (219-, 293-, and 366-m) sampling stations were combined by weighting the mean length at each age by the catch rate of Pacific ocean perch in that depth stratum and arriving at an overall weighted mean length for each age group (Table 3). The calculations were carried out separately for males and females, and the resulting age-length data were then fitted to the von Bertalanffy growth model using the technique described previously.

The results (Table 3) suggest that fish off Washington grow somewhat slower than those in Queen Charlotte Sound. In order for the results from the two stocks to be strictly comparable, however, several research cruises should have been made in Queen Charlotte Sound during September-December. The age-length data from those cruises where availability was maximal could then have been weighted in proportion to the catch rate for each depth stratum, as was done for the WVI stock. If fishermen effectively "sample" in proportion to abundance, however, the results from commercial fisheries data should agree well with those from research cruises.

ANNUAL CHANGES IN SIZE AND AGE COMPOSITION

Size Composition

Queen Charlotte Sound

The Washington State Department of Fisheries has obtained size composition data on landings from Queen Charlotte Sound since 1956. Collection of such data was limited and sporadic prior to

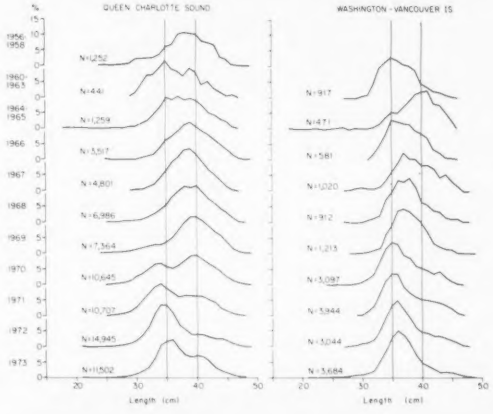

FIGURE 12.—Changes in the size composition (sexes combined) of Pacific ocean perch in commercial catches, 1956-73. N = number of fish sampled.

1967, but a good series of data, taken over the entire year, is available for each year during 1967-73.

Because a limited number of samples was available during 1956-66, it was frequently necessary to pool data from adjacent years when examining temporal trends in size composition. The results (Figure 12) furnish the only available estimates of the size composition of Pacific ocean perch in 1956-66 Washington trawl landings.

Collection of biological data was quite intensive during 1967-73, and it was possible to make allowances for the extensive seasonal changes in length and sex composition that occur in Queen Charlotte Sound. The Sound was treated as a single geographic unit, but size composition was determined separately for each of the four time strata previously discussed (January-April, May, June-August, and September-December). If few landings were made in one of these strata, it was combined with an adjacent stratum, and biological data from the latter were used to represent it. Table 4 shows the time strata used for each year's catch data, the landings in each stratum, and the amount of biological data collected.

Males and females differ in relative abundance and size composition, so they were treated separately. Mean weights of males and females in each time stratum were obtained by employing the length-weight relation (sexes combined) reported by Westrheim and Thomson (1971), together with the appropriate length frequencies in that stratum. The number of males and females landed in each stratum could then be estimated by dividing total pounds landed by the mean weight of fish in that stratum. These values were combined with size composition data to obtain the number of fish landed by time period, sex, and size group. Pooling these data by year and expressing the results in terms of percent frequency yielded the results shown in Figure 12.

TABLE 4.—Time strata used for analysis of 1966-73 size and age composition data from Queen Charlotte Sound. Pacific ocean perch catch by Washington trawlers (metric tons) and amount of biological data collected in each stratum are also shown.

Year	Time stratum	Washington trawl catch	Origin of biological data	Number of fish sampled for	
				Length-sex	Age
1966	Sept.-Dec.	2,723	Oct.-Dec.	3,517	1,419
1967	Mar.-May	868	May	1,104	433
	June-Aug.	2,817	June-Aug.	1,049	848
	Sept.-Dec.	1,656	Sept.-Dec.	2,648	1,183
1968	Jan.-Apr.	220	Jan.-Apr.	1,470	680
	May	842	May	1,310	505
	June-Aug.	1,870	June-Aug.	1,165	608
	Sept.-Dec.	1,855	Sept.-Nov.	3,041	1,011
1969	Jan.-May	687	May	648	298
	June-Aug.	2,205	June-Aug.	2,461	698
	Sept.-Dec.	2,099	Sept.-Dec.	4,255	714
1970	Jan.-May	546	Apr.-May	2,435	498
	June-Aug.	1,749	June-Aug.	4,214	649
	Sept.-Dec.	2,014	Oct.-Dec.	3,996	497
1971	Apr.-Aug.	1,446	May-Aug.	6,974	1,004
	Sept.-Dec.	1,480	Sept.-Dec.	3,733	1,232
1972	Apr.-May	379	May	3,174	887
	June-Aug.	1,568	June-Aug.	7,337	2,587
	Sept.-Dec.	1,417	Sept.-Nov.	4,434	1,321
1973	Mar.-Apr.	530	Apr.	2,940	942
	May	244	May	1,201	398
	June-Aug.	1,019	June-Aug.	5,058	1,658
	Sept.-Dec.	472	Sept.-Nov.	2,303	803

Substantial quantities of large Pacific ocean perch were present in Queen Charlotte Sound during 1956-58. Subsequent changes in size composition reflect changes caused by the commercial fishery and by recruitment of two strong series of year classes. The first series of year classes was centered around the 1952 year class and included the 1951-53 brood years (Westrheim et al. 1972). The presence of this series first became apparent in the 1960-63 landings, when the modal size was 35 cm—corresponding to an age of about 10 yr. The 1952 year class series caused the modal size to move progressively toward the right during 1960-70 (as its members grew in length), but seemed to have little influence on size composition in subsequent years. This is probably the cumulative result of large fishery removals during 1965-69, when the 1952 year class would have been 13-17 yr old.

A second series of strong year classes, centered around the 1961 and 1962 brood years (Westrheim et al. 1972) first showed up in the 1970 landings, when there was a secondary mode at 34 cm. This series of year classes came to dominate the landings during 1971-73, since the abundance of older fish had been drastically reduced by commercial fishing.

Washington-Vancouver Island

Size composition data from this region were more limited than data from Queen Charlotte Sound and it was never possible to analyze different time strata separately. All size composition data were summarized by year to produce the data in Figure 12. Data from 1956 to 1965 were especially limited and size composition data from adjacent years frequently had to be combined. This was done in such a manner that direct comparisons with Queen Charlotte Sound could be made.

Research surveys during 1965 (Westrheim

1970) suggested that the 1952 year class dominated here, as well as in Queen Charlotte Sound, and the results (Figure 12) tend to support this conclusion. The modal size was 35 cm for the 1960-63 period, and this corresponds to an age of about 10 yr. The 1966-67 size composition data also reflect the presence of a strong 1952 year class series, but is is not possible to follow the series past 1967. Extensive fisheries removals during 1966-68 resulted in sharply attenuated right-hand limbs for 1968-73 size composition curves, and the 1952 year class series was presumably swallowed up in these removals.

As in Queen Charlotte Sound, the strong 1961-62 year class series first showed up on the 1970 landings, when there was a mode at 35 cm. Because the biomass of older fish had been drastically reduced by the extensive fisheries removals of 1966-68, these year classes dominated the catches in the first year they appeared and in each subsequent year.

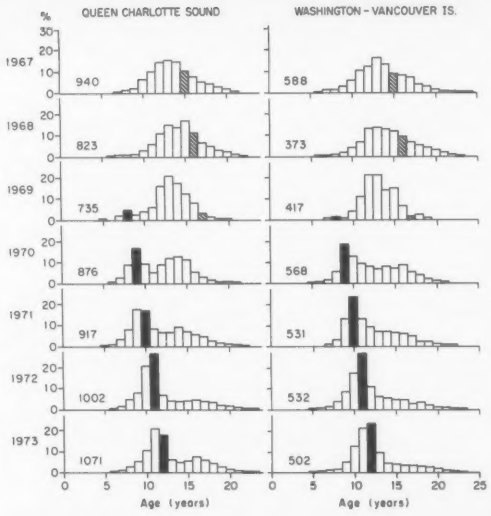

FIGURE 13.—Changes in the age composition (sexes combined) of Pacific ocean perch in commercial catches, 1967-73. The number of fish caught per hour is shown for each year, and the 1952 and 1961 year classes have been indicated by shading.

Age Composition

Queen Charlotte Sound

Age composition data for the Washington trawl landings from Queen Charlotte Sound have been collected since 1966. A series of data taken over the entire year is available for each year during 1967-73.

The procedure used to estimate the age composition of the 1967-73 landings was identical to that employed in the section on size composition. The number of fish landed in each time stratum was combined with the age-frequency data for that stratum to estimate the number of fish landed by age-group, sex, and time stratum. Pooling these data by year and dividing by the total Washington trawl effort expended in Queen Charlotte Sound yielded annual estimates of the number caught per hour, by age-group, and of percent age composition (Figure 13).

The 1952 year class series was centered around age 13 in 1965 and was almost fully vulnerable to fishing when the Queen Charlotte Sound fishery began its dramatic expansion. The cumulative effects of the extensive removals of 1966-67 were such that the 1951-53 year classes no longer dominated the catches after 1967-68. The 1952 year class series was exploited far more intensively than preceding year classes, and by the time the 1951-53 year classes were 17-19 yr old, they were less abundant than the relatively weak 1948-50 year classes had been at corresponding ages. This can be seen by comparing the abundance of 17-19 yr olds in 1970 (45 fish caught per hour) with their abundance in 1967 (118 fish caught per hour).

During 1970 and 1971, recruitment of the strong 1961 and 1962 year classes to the fishery restored the abundance of Pacific ocean perch to 1967 levels (Figure 13) and the number of fish caught per hour continued to increase through 1973. The condition of the QCS stock in 1973 was far from satisfactory, however, since it was made up of much younger fish than those characterizing even the 1967 stock.

Washington-Vancouver Island

No age composition data were available for Pacific ocean perch catches from the WVI stock until 1966, and it was not until 1967 that an adequate series of age composition samples was collected (Table 5). Age composition data on the WVI catches were quite limited, so no attempt was made to treat different time strata separately.

Age composition data for 1967-73 are remarkably similar to corresponding data from Queen Charlotte Sound (Figure 13). The harvests of 1966-68 sharply reduced the biomass of the 1952

TABLE 5.—Number of Pacific ocean perch from the WVI stock sampled for biological data.

Year	Length-sex	Age	Year	Length-sex	Age
1966	581	216	1970	3,089	1,124
1967	1,020	707	1971	3,944	1,460
1968	912	502	1972	3,044	1,036
1969	1,213	296	1973	3,684	1,335

year class series, which would have ranged from about 13 to 15 yr of age in 1966 and would have been almost fully vulnerable to trawling. Recruitment of the 1961 and 1962 year classes to the fishery began to restore abundance (as indicated by the number caught per fishing hour) to former levels and, as of 1970, the WVI stock was on the road to recovery. After 1970, however, the condition of the WVI stock followed an entirely different course than the QCS stock.

Exploitation rates for the QCS stock were low enough to allow an increase in abundance (number caught per hour) during 1970-73 (Figure 13), as the 1960-61 year classes became fully available to the fishery. Off Washington and Southwest Vancouver Island, however, exploitation rates remained at high levels during 1970-73, and the 1961-62 year classes were cropped off as soon as they recruited to the fishing grounds. Abundance consequently declined during 1970-73, opposite to the trend in Queen Charlotte Sound. The abundance of fish 15 yr and older was reduced below even 1970 levels, and 10 to 13 yr-old fish dominated the WVI stock as of 1973.

RECRUITMENT TO THE FISHERY

Consideration of the length-maximum girth data presented by Westrheim and Nash (1971) indicates that gear selection should begin at a relatively small size. The internal (between-knot) measure of the cod end mesh size commonly used by Washington trawlers is about 3.25 inches (8.26 cm) and the smallest fish retained should have a girth of $2 \times 3.25 = 6.5$ inches. This assumes that escape is not facilitated by compressability on the one hand and that the rigidity of the trawl meshes does not hinder escape on the other. If these assumptions are valid, and the girth at 50% retention is 6.5 inches, Westrheim and Nash's results show that the 50% selection length should be 24.5 cm.

A 25.4-cm fish would be too small for market acceptance, but previous comparisons of Pacific ocean perch size composition in research catches and commercial landings (Gunderson 1972) have indicated that 50% of all 32- to 34-cm fish on the grounds are retained by Washington trawlers. Virtually all fish 36 cm and larger are retained by the fishermen. Reference to the age-length information in Table 3 shows that the length at 50% retention corresponds to an age of about 8 or 9 yr, and that all fish older than 11 yr would be retained. Slight between-stock differences in retention would be expected, owing to differences in growth rate.

Despite the fact that all fish older than age 10 are vulnerable to the fishing gear in use, and large enough that almost all are retained for market sales, age composition data from commercial catches (Figure 13) and research surveys (Gunderson 1974) show that recruitment to the fishing grounds is not complete until much later than age 10. On the assumption that the modal age of the catch lies near the first year in which recruitment is complete, these data would imply that full recruitment could occur anywhere from age 11 to 14.

The high variability in modal size is caused by year to year variation in availability, year class strength, and fishing mortality, and one way to reduce its significance is to deal with long-term averages of relative abundance. In order to do this, a relative abundance index (U_i) was calculated for each age group using the 1967-73 age composition data for the QCS and WVI stocks. This index was calculated as:

$$U_i = \frac{1}{7} \sum_{n=1967}^{1973} \left(\frac{C}{f}\right)_n$$

where U_i = the relative abundance of the ith age-group and $\left(\frac{C}{f}\right)$ = the number of fish in the ith age-group caught per hour. Percentage age composition during 1967-73 has been calculated from these U_i data and is shown by stock in Figure 14.

The results show that although the modal age in both stocks is 11 yr, recruitment to the fishing grounds is quite gradual. In fact, it is not until age 15 that the full force of fishing mortality seems to be exerted on any given year class. Estimates of the exact proportion of the fish in each age-group that have recruited to the fishing grounds, and are vulnerable to fishing, can be derived from U_i values, starting with the relation:

$$C_i = uV_iN_i$$

where C_i = catch of fish in the ith age-group

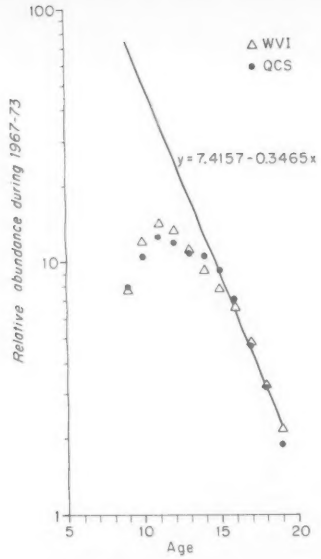

FIGURE 14.—Relative abundance of age groups 5-19 during 1967-73, for the QCS and WVI stocks of Pacific ocean perch.

u = exploitation rate
V_i = proportion of population vulnerable at age i
N_i = total number of fish in the ith age-group.

Similarly, $C_{i+1} = uV_{i+1}N_{i+1} = uV_{i+1}N_i \exp -(V_i F + M)$ if we assume that V_i remains constant throughout the year, and:

$$\frac{U_i}{U_{i+1}} \approx \frac{C_i}{C_{i+1}} = \frac{V_i}{V_{i+1} \exp -(V_i F + M)}.$$

This equation can be solved iteratively for V_i if we have estimates of F (fishing mortality). M (natural mortality), V_{i+1}, and the ratio U_i/U_{i+1}.

The estimates of Z (total instantaneous mortality) and F were derived directly from the data in Figure 14. Trends in the relative abundance of 15-19 yr olds were quite similar in the QCS and WVI stocks, and Z was estimated by fitting a common regression line to the data for both stocks. The resulting regression equation for 15-19 yr olds was:

$$\log Y = 7.4157 - 0.3456X,$$

where Y = relative abundance during 1967-73, expressed as percent frequency
X = age in years.

The slope of this line (0.35) was used to represent Z for fully recruited age-groups. This was then separated into F and M by assuming a known value for M.

Estimation of V_i schedules began by assuming that the vulnerability coefficient for 16 yr olds (V_{16}) was 1.0. Using the QCS data, and $M = 0.12$ for example:

$$\frac{U_{15}}{U_{16}} = 1.31 = \frac{V_{15}}{1.0 \exp -(0.23\ V_{15} + 0.12)}.$$

By iteration, it was determined that $V_{15} = 0.94$ and this value was used to determine V_{14} from:

$$\frac{U_{14}}{U_{15}} = 1.14 = \frac{V_{14}}{0.94 \exp -(0.23\ V_{14} + 0.12)}.$$

Again this was solved iteratively, giving $V_{14} = 0.79$. Proceeding backwards, the vulnerability coefficients for Queen Charlotte Sound were estimated for all age-groups 10 and older. The calculations could not be carried past age 10, since younger age-groups may be subject to substantial rates of discard by fishermen.

Estimates of the V_i schedules for both the QCS and WVI stocks are shown in Table 6. Calculations were carried out for $M = 0.15$, $F = 0.20$ as well as for $M = 0.12$, but this had little effect on the estimates of vulnerability. The geometric means of the vulnerability coefficients obtained by assuming different values of M have been plotted graphically in Figure 15 and suggests that the proportion recruited to the fishery is a linear function of age. There is no obvious reason why this should be so, however, and no attempt was made to fit a straight line (or lines) to these data, or to extend the relationship to fish less than 10 yr old. The geometric means of the V_i estimates were used directly in all later work.

TABLE 6.—Proportion of Pacific ocean perch population vulnerable to fishing, by age-group and stock.

Stock	M	10	11	12	13	14	15	16
QCS	0.12	0.32	0.45	0.53	0.62	0.79	0.94	1.00
	0.15	0.30	0.43	0.52	0.61	0.78	0.94	1.00
	Mean	0.31	0.44	0.53	0.62	0.79	0.94	1.00
WVI	0.12	0.36	0.53	0.64	0.69	0.75	0.87	1.00
	0.15	0.34	0.51	0.63	0.68	0.75	0.87	1.00
	Mean	0.35	0.52	0.64	0.69	0.75	0.87	1.00

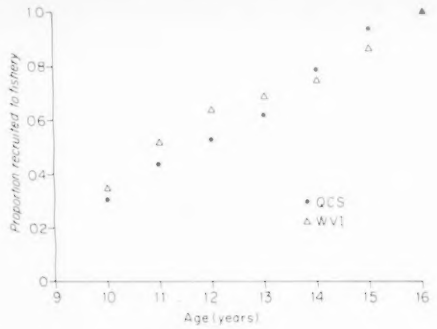

FIGURE 15.—Estimated proportion of each age group recruited to the fishing grounds, for the QCS and WVI stocks of Pacific ocean perch.

MORTALITY

All estimates of Pacific ocean perch mortality rates depend on a knowledge of the age structure of the population. Virtually all fish caught die from the effects of decompression, so that no successful tagging studies have ever been carried out.

In this section, data on number caught per hour by age-group were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year n to ages 15-19 in year $n + 1$, or to ages 16-20 in year $n + 2$. These age-groups were chosen so as to strike a balance between problems with incomplete recruitment on the one hand and age determination problems on the other. Previous analysis has suggested that recruitment is not complete until age 16, about the same time that age determination becomes difficult (Table 7) and the ages of some individuals are presumably underestimated. No age-groups older than 20 should be included in survival estimates, and restricting mortality estimates to fully recruited age-groups (16-19 yr olds) could result in underestimation of survival rates. Inclusion of the incompletely recruited 14 and 15 yr olds offset this to some degree and had the additional benefit of basing the survival estimates on five age-groups rather than three.

All survival estimates were expressed on an annual basis (S), and then used to estimate Z. On the assumption that M is density independent and that F is a linear function of total hours trawled, the model $Z = q\bar{f} + M$, where q = proportion of population caught by trawling 1 h and $\bar{f}$ = mean annual number of hours trawled, was employed. Linear regression of Z on $\bar{f}$ yields estimates of q and M where the model is appropriate.

Total international fishing effort (f) was estimated by dividing the total international catch in a given year by the corresponding CPUE for the Washington trawl fleet (after Gulland 1969). The value of $\bar{f}$ was obtained by averaging f over the years that each estimate of Z pertained to.

Queen Charlotte Sound

Calculation of total international fishing effort is outlined in Table 8. The 1967-72 Soviet catch data for the INPFC Charlotte area was taken from unpublished analyses by T. A. Dark and N. B. Parks. These data were derived from analysis of fleet location and catch by quarter and give the most detailed breakdown of the Soviet catch that is currently available. Soviet catch estimates for 1965, 1966, 1972, and 1973, as well as all Japanese and North American data for the years 1963-73, were derived from Westrheim et al. (1972) and a recent update of that report.

Estimates of Z are plotted against mean international fishing effort (Table 8) in Figure 16 and the results indicate that the information collected so far can provide only tentative estimates of M. Pacific ocean perch vary widely in their availability to on-bottom trawls and the CPUE indices used in mortality estimation are consequently suscep-

TABLE 7.—Deviations of Canada's final otolith readings from those of United States, by age-group, for a collection of Pacific ocean perch from Queen Charlotte Sound, June 1972.[1]

Deviations from Washington	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	22	25	Total	Percent
+5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	3	3.6
+4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	1	4	4.8
+3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	2	2.4
+2	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	2	—	1	—	—	—	5	6.0
+1	—	—	—	—	—	—	—	—	—	—	3	1	1	2	—	1	—	—	—	—	—	8	9.5
0	6	11	10	4	4	3	1	3	2	9	4	—	—	—	2	—	—	—	—	—	—	59	70.2
−1	—	—	—	—	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	3	3.6
Total	6	11	10	4	5	3	1	3	3	11	7	2	1	2	2	4	1	1	2	4	1	84	100.1

[1]S. J. Westrheim and W. R. Harling. 1973. Report on the 1972 comparison of Pacific ocean perch otolith and scale interpretations. Unpubl. manuscr., 24 p.

TABLE 8.—Calculation of total international fishing effort for Pacific ocean perch in Queen Charlotte Sound and the INPFC Vancouver area.

Year	Catch (metric tons) U.S.-Can.	Jap.	U.S.S.R.	Total	Washington CPUE (metric tons/hour)	Total international effort (Wash. hours)
			Queen Charlotte Sound			
1963	3,712			3,712	0.841	4,414
1964	3,507			3,507	0.731	4,798
1965	4,889		7,000	11,889	1.040	11,432
1966	8,254	few	18,800	27,054	1.132	23,899
1967	5,745	3,196	17,800	26,741	0.800	33,426
1968	6,051	5,614	1,827	13,492	0.722	18,687
1969	6,628	6,268	55	12,951	0.656	19,742
1970	6,077	3,775	2	9,854	0.714	13,801
1971	4,165	702	few	4,867	0.670	7,264
1972	5,561	2,281	0	7,842	0.710	11,045
1973	3,626	958	0	4,584	0.812	5,644
			Vancouver area			
1966	2,358	few	14,000	16,358	0.640	25,559
1967	805	6,678	10,263	17,746	0.434	40,889
1968	552	4,751	4,602	9,905	0.247	40,101
1969	583	1,787	2,143	4,513	0.242	18,649
1970	1,955	2,186	814	4,955	0.298	16,628
1971	1,155	1,838	1,145	4,138	0.317	13,054
1972	624	1,580	878	3,082	0.312	9,878
1973	344	2,989	490	3,823	0.228	16,768

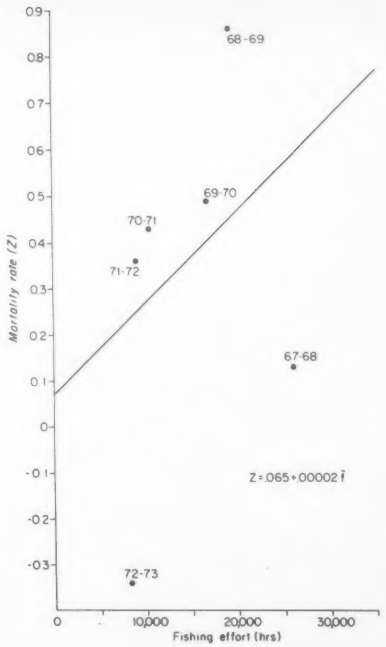

FIGURE 16.—Relation between total instantaneous mortality rate (Z) and fishing effort for the QCS stock of Pacific ocean perch, based on data from the Washington trawl fleet.

tible to fluctuations that have no relation to abundance. Fluctuations of this nature were responsible for much of the variability in Figure 16 and resulted in negative mortality estimates for 1972-73. The low quality of the data on international catch (especially U.S.S.R. data) also contributed to this variability, however.

Linear regression was carried out for the data in Figure 16, and the resulting estimates of M and q were 0.065 and 0.00002, respectively. As expected, correlation between Z and f was quite low (r = 0.30).

Washington-Vancouver Island

Calculation of international effort in the INPFC Vancouver Area is outlined in Table 8. The data sources used to estimate total international effort are the same as for Queen Charlotte Sound.

Annual estimates of Z are plotted against mean international effort in Figure 17. Research cruises off Washington (Gunderson 1974) have shown that extreme fluctuations in the availability of Pacific ocean perch occur here and that changes in the age composition of the catch seem to be associated with them. As in Queen Charlotte Sound, these changes in availability, together with the low quality of the international effort data, generate a high degree of variability in the relation between Z and $\bar{f}$. Correlation between these variables was higher than in Queen Charlotte Sound (r = 0.49), however, and the data seemed to conform more closely to the model proposed. Linear regression analysis resulted in estimates of M = 0.232 and q = 0.00001 for the WVI stock.

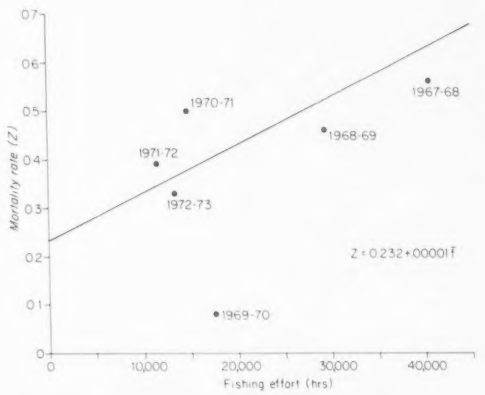

FIGURE 17.—Relation between total instantaneous mortality rate (Z) and fishing effort for the WVI stock of Pacific ocean perch, based on data from the Washington trawl fleet.

The estimate of M obtained for the WVI stock agrees well with an estimate obtained by Chikuni (1975). Chikuni used CPUE and age composition data from the Japanese trawl fleet, and estimated M to be 0.227 for Pacific ocean perch in the Oregon-British Columbia region.

The general applicability of the $Z = q\bar{f} + M$ model for both the QCS and WVI stocks was encouraging and suggests that further collection of data on mortality rates should give increasingly more reliable estimates of M. At present, however, it probably is unwise to overemphasize the between-stock differences found in natural mortality. The results of the current study should be regarded as somewhat tentative and serve mainly to show that M in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

SEXUAL MATURATION

Maturity Criteria Used

Seasonal changes in the gross morphology of Pacific ocean perch gonads have previously been used to describe the reproductive cycle in the Washington-Queen Charlotte Sound region (Gunderson 1971; Snytko 1971). This technique was again employed in this study, and, during 1968-73, 9,548 mature fish were classified as to maturity state using the criteria in Table 9.

Mating and insemination activities cause a reduction in the proportion of males whose gonads are swollen with sperm (Stage 3), and seem to occur during August-September in both the QCS and WVI stocks (Table 10). About 3 mo pass before ovulation and fertilization of eggs occur, and this is first detectable when females in maturity Stage 4 are encountered. Embryonic development begins after fertilization and continues for about 2 mo before embryos are released.

TABLE 9.—Description of the stages used to describe Pacific ocean perch maturity.

Maturity		
Code	Stage	Description of gonads
		Males
1	Immature	Stringlike, translucent
9	Maturing	Stringlike, translucent brown or white
8	Resting	Ribbonlike, triangular in cross-section, brown or white
3	Large white	Large and swollen, somewhat rounded in cross-section, glistening white
		Females
1	Immature	Ovary small and translucent
2	Maturing	Ovary small and yellow
3	Large yellow	Ovary firm, oocytes yellowish and opaque
4	Yolk cleared (eggs fertilized)	Ovary not firm, eggs yellowish and translucent
5	Eyed embryos or larvae	Ovary not firm, eggs translucent with black dots or visible larvae
6	Spent	Ovary large and flaccid with a red, purple, or dark gray color
7	Resting	Ovary firm, gray or pink, some with black blotches.

The peak of the embryo-release period occurs during March in the WVI stock (Table 10). Most of the females examined in February were in the "fertilized" stage (Stage 4), while most of those examined during April were in the "resting" stage (Stage 7). Few observations could be made for QCS females during February-April, but the results suggest that embryo release occurs near March. The relatively high proportion of recently spent fish (Stage 6) encountered during May suggests that spawning occurs somewhat later in Queen Charlotte Sound than it does off Washington and southwest Vancouver Island.

Age and size at first maturity should be determined during the period when mature gonads are most fully developed, near August-September for males and near March for females. The central problem in determining length or age at maturity is the status of "maturing" fish (Table 9), and further work was carried out to determine whether or not these fish are sexually mature. Two hundred sixteen fish covering a broad range of lengths were selected from the 1971-72 commercial landings for this purpose. The length (centimeters), sex, and weight (decigrams) of each fish were determined, and the gonads classified as to maturity state. The gonads were then removed from the fish and weighed to the nearest 0.01 g. The results (Figure 18) were expressed in terms of relative gonad weight (g), where

$$g = \frac{\text{gonad weight (grams)}}{\text{body weight (grams)}} \times 10^2$$

i.e.; gonad weight expressed as a percentage of body weight.

Males

Between-season comparisons show that the relative gonad weights of "maturing" males are virtually the same during the mating season (August-September) as they are during March, when all male gonads are in a quiescent state. These fish are obviously immature and seasonal changes in their relative gonad weight contrast sharply with those of adult fish. Fish classified as "maturing" should therefore be grouped with

TABLE 10.—Percentage of adult Pacific Ocean perch in each maturity stage, by stock, during 1968-73.

Item	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Males:				QCS Stock							
Total examined		231		339	659	486	279	328	407	430	340
Percent in each maturity stage:											
Stage 8		100		100	99	71	27	58	55	82	100
Stage 3					1	29	73	42	45	18	
Total		100		100	100	100	100	100	100	100	100
Females:											
Total examined		7		11	219	364	212	358	442	675	512
Percent in each maturity stage:											
Stage 3		71		18		18	63	75	99	100	99
Stage 4				9							1
Stage 5				18	1						
Stage 6		14			18	2	2	1			
Stage 7		14		55	80	80	35	25	1		
Total		99		100	99	100	100	101	100	100	100
Males:					WVI Stock						
Total examined		234	223	448			[1]183	151	102		225
Percent in each maturity stage:											
Stage 8		100	100	100			26	32	65		100
Stage 3							74	68	35		
Total		100	100	100			100	100	100		100
Females:											
Total examined	[1]101	197	213	537			[1]129	178	118		210
Percent in each maturity stage:											
Stage 3	30	4	1	1			78	100	100		100
Stage 4	69	63	11								
Stage 5	2	30	43	4							
Stage 6		2	15	14							
Stage 7		1	30	81			22				
Total	101	100	100	100			100	100	100		100

[1]All fish examined during this month came from research vessel catches.

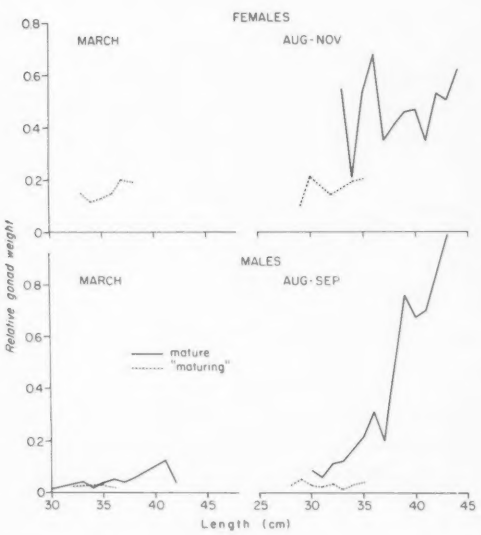

FIGURE 18.—Seasonal changes in the relative gonad weight of mature and "maturing" Pacific ocean perch by length group and sex.

"immature" males in all analysis of length or age at maturity.

There was considerable overlap in the relative gonad weight of mature and "maturing" males during March. Relative gonad weight of adult males examined during the mating season increased exponentially with size, however, so that mature and immature fish were readily differentiated for fish longer than about 32 cm. For smaller fish, however, the relative size of the gonad was not sufficient to determine whether or not a fish was mature, and color had to be relied on to a large degree. If the gonads were white rather than brown, this was taken to indicate the presence of developing sperm and the fish was classified as mature. Whether or not these small males actually participate in mating remains an unanswered question, however.

Because mature and "maturing" males were most readily differentiated when mature fish had white, swollen gonads, only data collected during June-October were used to determine size and age at maturity. The data in Table 10 show that significant quantities of males with Stage 3 gonads were found during this period.

Females

Female gonads are difficult to weigh during the embryo release period, since they are easily ruptured then. Furthermore, eggs and embryos can be extruded with slight pressure on the body cavity during this period, and it is possible that significant quantities of these sex products are lost when fish are compacted in the cod end of a trawl. For these reasons, no data on gonad weight of mature females were taken during March.

Between-season comparisons for "maturing" females (Figure 18) show that their relative gonad weights were virtually the same during August-November as they were during the embryo release period in March. This is conclusive evidence that "maturing" fish are not sexually active, and they were grouped with immature fish in all later analysis.

Differentiation of "maturing" and mature fish was less difficult for females than for males. It was most difficult during July-November, when most adult fish were in maturity Class 3 (Table 10), and had gonads that were similar to "maturing" gonads in color. There was also some overlap in the relative gonad weights of mature and "maturing" individuals of the same length during this period (Figure 18).

During the embryo release period, or when females were in the resting state, adult gonads were readily differentiated from the small, yellowish gonads of "maturing" fish. Consequently, only maturity data collected during February-June were used to examine the size and age at first maturity for females.

Length and Age at Maturity

Data on maturity of Pacific ocean perch have been gathered since 1968, during the course of routine biological sampling of commercial catches. In addition, some maturity data were available from research cruises off the northern Washington coast. The data for 1968-72 combined were examined by stock to determine size and age at maturity.

In most instances, age, length, and maturity data were available for individual fish, and the proportion of mature fish in each cell of an age-length matrix could be calculated. This type of analysis was carried out for both males and females from Queen Charlotte Sound (Tables 11, 12) and for females off Washington and southwest Vancouver Island (Table 13).

Only 213 age-length-maturity observations were available for WVI males, too few to allow direct analysis of maturation by age-groups. Examination of the relation between length and maturity was possible, however, as 551 length-maturity observations were available.

Length-maturity relation

Tables 11 through 13 show the proportion of mature fish in each cell of an age-length matrix. The region in which 50-80% of the fish were mature is delineated by the isopleths drawn in these tables and can be interpreted as a maturity response surface. For all three sets of data, the 50-80% region occupied a narrow range of size groups (3-5 cm) and a relatively wide range of age-groups (5-6 yr). Hence it seems that maturation of both male and female Pacific ocean perch depends more on the size of a fish than its age.

Raw data on length versus proportion mature were plotted for each area and sex (Figure 19) and seemed to conform to a logistic equation (Finney 1971) of the form:

$$P_l = \frac{1}{1 + \exp - \left(\frac{l - l_{0.50}}{\sigma}\right)}$$

where l = length in centimeters
P_l = proportion mature at length l
$l_{0.50}$ = length where: $P_l = 0.5$ = maturation length
σ = constant.

The length-maturity curves are quite steep in the vicinity of $P_l = 0.2$-0.8 and maturation can be regarded as knife-edged, taking place at $l_{0.50}$. Because the above equation is symmetrical about $l_{0.50}$, the area under the curve and to the left of $l_{0.50}$ is equal to the area above the curve and to the right of it. Hence, the errors introduced by assuming knife-edged maturation at $l_{0.50}$ tend to balance.

By algebraic manipulation, the above equation can be linearized to:

$$\ln\left(\frac{1}{P_l} - 1\right) = \frac{l_{0.50}}{\sigma} - \frac{l}{\sigma} .$$

The equation was then in the form $y = \alpha + \beta l$ and

TABLE 11.—Proportion mature in each length and age-group, for female Pacific ocean perch from the QCS stock. Cells with only one observation were not considered.

Length (cm)	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
22														1
24													0.00	2
25			0.00										0.00	3
26			0.00										0.00	3
27			0.00										0.00	4
28			0.00	0.00									0.00	10
29		0.00	0.00	0.00	0.00								0.00	23
30			0.00	0.00	0.00								0.00	20
31			0.00	0.00	0.00	0.00	0.00						0.00	45
32				0.00	0.06	0.00	0.00	0.05					0.04	79
33			0.00	0.20	0.09	0.04	0.00	0.00					0.07	85
34				0.00	0.03	0.15	0.11	0.25	0.00				0.09	90
35				0.00	0.22	0.48	0.27	0.30	0.00				0.29	85
36				0.00	0.56	0.32	0.28	0.64	0.67	1.00	1.00		0.44	87
37					1.00	0.56	0.92	0.56	0.57	0.83	1.00		0.68	73
38						0.67	0.64	0.83	0.75	0.82	1.00		0.74	53
39							1.00	0.83	1.00	1.00	0.88		0.95	60
40							0.89	1.00	1.00	0.90	1.00	1.00	0.95	66
41								1.00	1.00	1.00	0.95	0.88	0.97	69
42								1.00	1.00	1.00	1.00	0.93	0.99	75
43									1.00	1.00	1.00	1.00	1.00	65
44									1.00	1.00	1.00	1.00	1.00	53
45									1.00	1.00	1.00	1.00	1.00	28
46											1.00	1.00	1.00	11
47												1.00	1.00	4
49														1
Proportion mature by age		0.00	0.00	0.03	0.13	0.25	0.37	0.64	0.81	0.96	0.97	0.95		
Number examined	1	4	35	75	152	143	139	77	116	135	108	110		

TABLE 12.—Proportion mature in each length and age-group, for Pacific ocean perch males from the QCS stock. Cells with only one observation were not considered.

Length (cm)	≤4	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
21															1
23															1
24															1
25														0.33	3
26		0.00		0.00	0.33									0.14	7
27			0.00	0.00										0.00	7
28				0.00										0.00	6
29			0.00	0.00	0.00	0.50								0.10	21
30				0.40	0.25	0.50								0.33	21
31				0.80	0.57	0.61	0.64	0.50						0.61	59
32				0.50	0.61	0.80	0.69	1.00						0.75	67
33					0.69	0.97	0.94	0.92						0.91	113
34				1.00	1.00	0.97	0.93	0.93	0.88	1.00				0.94	166
35					1.00	1.00	0.98	1.00	1.00	1.00	1.00			0.99	150
36						1.00	0.94	0.98	1.00	1.00	1.00	1.00		0.98	157
37						1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.99	167
38							1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	202
39							1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	207
40								1.00	1.00	1.00	1.00	1.00	1.00	1.00	224
41									1.00	1.00	1.00	1.00	1.00	1.00	149
42									1.00	1.00	1.00	1.00	1.00	1.00	77
43											1.00	1.00	1.00	1.00	29
44													1.00	1.00	5
45													1.00	1.00	2
Proportion mature by age		0.00	0.14	0.29	0.56	0.89	0.92	0.97	0.98	1.00	1.00	1.00	1.00		
Number examined	1	5	7	34	94	150	225	230	241	250	217	158	230		

the data in Tables 11-13 could be used in weighted linear regression of $\ln[(1/P_l) - 1]$ on l. The weights used for y observations were $1/\mathrm{Var}(y) = nP_l(1 - P_l)$. Regression coefficients obtained were then used to estimate $l_{0.50}$ $(-\alpha/\beta)$ and σ $(-1/\beta)$.

These estimates were made by sex for Pacific

TABLE 13.—Proportion mature in each length and age-group, for female Pacific ocean perch from the WVI stock. Cells with only one observation were not considered.

Length (cm)	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
28		0.00										0.00	3
29												0.00	2
30		0.00										0.00	3
31			0.00									0.00	5
32				0.00	0.00							0.00	7
33			0.67		0.00	0.00	1.00					0.33	15
34				0.40	0.38	0.25	0.57	1.00	0.50			0.44	32
35				0.33	0.59	0.70	0.67	1.00	1.00	1.00		0.65	46
36		1.00		0.67	0.77	0.50	0.92	0.88	0.85	1.00	0.80	0.79	100
37			1.00	1.00	0.75	0.70	0.95	1.00	0.83	0.80	1.00	0.87	105
38				0.75	0.89	1.00	0.86	1.00	1.00	1.00	1.00	0.97	123
39					1.00	1.00	0.88	1.00	0.93	1.00	1.00	0.97	111
40							1.00	1.00	1.00	1.00	1.00	1.00	65
41							1.00	1.00	1.00	1.00	1.00	1.00	69
42									1.00	1.00	1.00	1.00	34
43									1.00	1.00	1.00	1.00	46
44									1.00		1.00	1.00	26
45											1.00	1.00	13
46											1.00	1.00	11
47											1.00	1.00	2
48											1.00	1.00	2
49											1.00	1.00	1
Proportion mature by age	0.33	0.25	0.42	0.46	0.60	0.65	0.87	0.98	0.94	0.98	1.00		
Number examined	3	8	12	24	67	81	101	105	103	98	219		

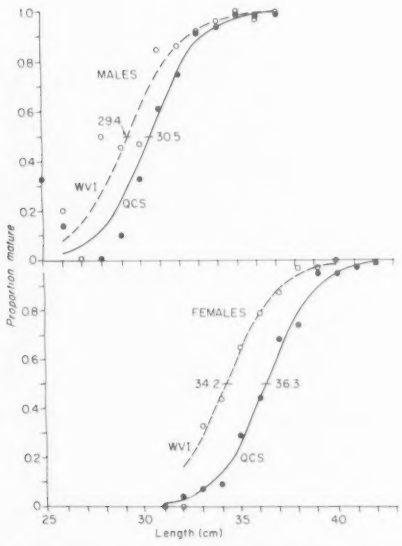

FIGURE 19.—Length-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

ocean perch in the QCS and WVI stocks (Table 14). Predicted curves for proportion mature at each length have been calculated and are represented by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 19. These curves, and the $l_{0.50}$ estimates they are based on, indicate that both

TABLE 14.—Estimated values of parameters for the equations used to examine length and age at maturity for Pacific ocean perch.

Item	Males		Females	
	QCS stock	WVI stock	QCS stock	WVI stock
	Length at Maturity			
$l_{0.50}$	30.4627	29.3782	36.2705	34.2335
σ	1.2791	1.4170	1.2405	1.3252
Var ($l_{0.50}$)	0.0492	0.0809	0.0105	0.0316
Z statistic[1]	3.0067		9.9277	
	Age at Maturity			
$t_{0.50}$	7.5884	—	11.3775	9.2899
σ	0.9799	—	1.1819	1.6132
Var ($t_{0.50}$)	0.0543	—	0.0204	0.1068
Z statistic[2]	—		5.8533	
$t_{0.50}$	7.0	6.5	10.3	10.0

[1]For test of between-stock differences in $l_{0.50}$.
[2]For test of between-stock differences in $t_{0.50}$.

males and females mature at a much smaller size off Washington and Southwest Vancouver Island than they do in Queen Charlotte Sound.

In order to examine the significance of between-area differences further, the variance of $l_{0.50}$ was approximated by using the delta method:

$$\text{Var}\,(l_{0.50}) = \text{Var}\left(\frac{-\alpha}{\beta}\right) = \frac{1}{\beta^2}\,(\text{Var}\,\alpha) + \frac{\alpha^2}{\beta^4}\,\text{Var}\,(\beta) - 2\,\frac{\alpha}{\beta^3}\,\text{Cov}\,(\alpha, \beta).$$

This variance was estimated for each sex and area considered (Table 14) using information from

the linear regression program previously employed. If it is assumed that the estimates of $l_{0.50}$ are normally distributed, then the quantity

$$\frac{\frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta_2}}{\sqrt{\mathrm{Var}\left(\frac{\alpha_1}{\beta_1}\right) + \mathrm{Var}\left(\frac{\alpha_2}{\beta_2}\right)}}$$

is distributed as Z and can be used to test the hypothesis that there is no difference in $l_{0.50}$ between areas. The Z values obtained for both males and females (Table 14) indicate that the observed differences in length at maturity are highly significant, since $P(Z>3.0067) = 0.0013$ and $P(Z>9.9277) \approx 0$ under the hypothesis being tested.

Age-maturity relation

Age at maturity was estimated by two methods. The first series of estimates was developed by using the logistic equation:

$$P_t = \frac{1}{1 + \exp -\left(\frac{t - t_{0.50}}{\sigma}\right)}$$

where P_t = proportion mature at age t
$t_{0.50}$ = age when $P_t = 0.50$ = age at maturity
σ = constant.

The parameters for this equation were estimated in the same manner described in the length-maturity section, through weighted linear regression analysis of the data in Tables 11-13. The resulting estimates of $t_{0.50}$ and σ are shown in Table 14, and the predicted relationships between P_t and t are shown by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 20. The $t_{0.50}$ estimates obtained in this way are estimates of the age when males mate for the first time and when females release their first brood of embryos. The Z statistic shows that between-stock differences in age at first brood release were statistically significant, since $P(Z>5.8533) \approx 0$.

A second series of estimates for the age at maturity ($t'_{0.50}$) was obtained by utilizing the $l_{0.50}$ values obtained in the previous section, and von Bertalanffy growth parameters from Table 3. The equation used was:

$$t'_{0.50} = t_0 - \frac{1}{K} \ln\left(1 - \frac{l_{0.50}}{L_\infty}\right)$$

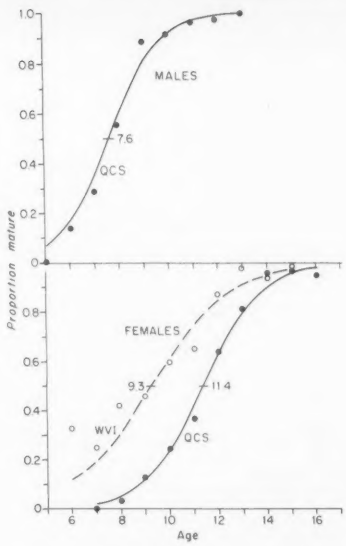

FIGURE 20.—Age-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

Resulting estimates for males (Table 14) are probably quite accurate, since both $l_{0.50}$ and the age-length relations in Table 3 were based on data collected during June-December (near the mating season). The $t'_{0.50}$ estimates for females are biased, however, since a significant amount of growth occurs between the period when $l_{0.50}$ was estimated (February-June) and the period when the age-length data were collected (July for the WVI stock, September-December for the QCS). The bias is relatively small for the WVI stock, but in Queen Charlotte Sound most of the annual growth probably occurs during the intervening time period. The $t'_{0.50}$ value obtained for QCS females consequently underestimates age at first brood release by almost a year.

The results from both methods used to estimate age at maturity (Table 14) indicate that both males and females mature at an earlier age off Washington and southwest Vancouver Island than they do in Queen Charlotte Sound. When biases in $t'_{0.50}$ are considered, it appears that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. Estimates of age at first mating for males were not subject to the same bias as those for females and can be taken directly from Table 14. These results suggest that males first mate at age 6

in the WVI stock and age 7 in Queen Charlotte Sound.

FECUNDITY

Methods Used in Fecundity Determination

Collection of Ovaries

Previous fecundity work on *Sebastes* has indicated that the time of ovary collection must be carefully controlled. Lisovenko (1965) determined fecundity for two groups of Pacific ocean perch in the Gulf of Alaska, the first consisting of 61 fish collected prior to fertilization and the second of 29 fish with fertilized ova. He found that the estimated fecundity of the first group was 1.5-2.0 times higher than that of the second, considering females of comparable size. Lisovenko attributed this difference to eggs bursting when females were hauled to the surface, but accidental extrusion of the fertilized eggs could also have beem implicated. Pacific ocean perch containing fertilized eggs can be made to extrude these eggs by slight pressure on the body cavity and make poor specimens for determination of fecundity.

If ovary samples are collected too far in advance of fertilization, however, maturing oocytes that will be fertilized in the fall are too small to be differentiated from immature oocytes. The optimal time to collect material for fecundity observations is therefore August-November, when immature and maturing oocytes can be differentiated, but fertilization of ova has not yet occurred.

Collection dates and times for fecundity samples used in this study are shown below:

Date (1973)	*Location*	*Number collected*
22 Aug.	Destruction Island, Wash.	14
26 Aug.	Tillamook Head, Oreg.	27
19 Sept.	S.E. Corner, Goose Island	40

All fish from Queen Charlotte Sound were taken from the landings of a commercial trawler, while those from the southern region were collected aboard the U.S.S.R. research trawler *Seskar*. The cruise objectives of the *Seskar* were such that only limited quantities of Pacific ocean perch were caught off Washington, and collections made off the Oregon coast were used to supplement those from the WVI stock.

Since between-area fecundity comparisons were to be made, the attempt was made to collect ovaries from Queen Charlotte Sound when the fish were in the same stage of the reproductive cycle as those off Washington and Oregon. Despite this, gross examination of male gonads and data on oocyte diameters (Gunderson 1976) indicated that fish in the Queen Charlotte Sound collection were not quite as advanced as those collected 1 mo earlier off Washington and Oregon.

All ovaries collected were placed in modified Gilson's solution (Bagenal and Braum 1968) to harden the eggs and separate them from surrounding ovarian tissue. After about 1 mo, ovarian tissue was removed from the eggs and the fluid was changed. After the samples had been in Gilson's solution for a total of 3 mo, they were removed and stored permanently in 10% ethyl alcohol.

Differentiation of Mature and Immature Oocytes

A series of ovaries was collected over the whole range of the reproductive cycle so that the growth progression of maturing oocytes could be followed. All specimens were collected in the Washington-Oregon region and their ovaries were placed in Gilson's solution until the oocytes separated from ovarian tissue. Subsampling of the eggs in an ovary was accomplished by the same technique used to estimate fecundity (described below).

The size frequency for the eggs in a specimen was obtained by systematically measuring (nearest 0.01 mm) those eggs lying on transect lines drawn on a Petri dish, until a desired sample size had been attained. Many of the eggs were elliptical or irregularly shaped and, in these cases, the longest axis parallel to the counting scale was selected for measurement. One specimen was in the "embryo or eyed larvae" stage of maturity and, in this particular instance, all eggs with embryos were measured along the longitudinal axis of the embryo.

The results (Figure 21) showed that there was a significant overlap in the size of immature and maturing oocytes during the period when fecundity samples were collected. By October, the size of maturing oocytes had increased substantially and differentiation of maturing oocytes was straightforward. Following fertilization of the first brood, however, it appears that other groups of oocytes begin to mature, so that several sizes of eggs and embryos are present in ovaries that have

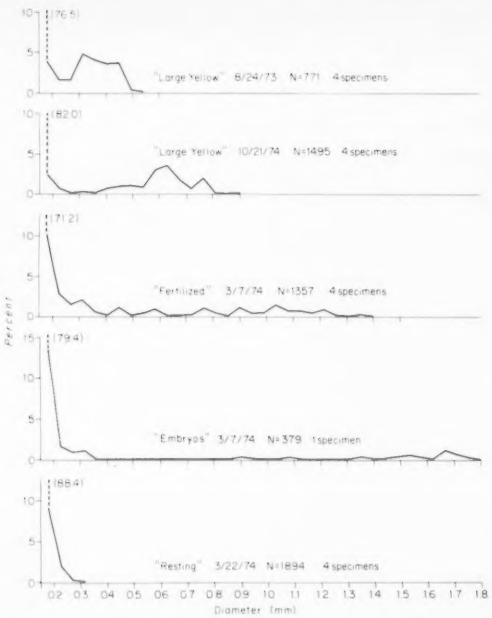
(76.5)
"Large Yellow" 8/24/73 N=771 4 specimens
(82.0)
"Large Yellow" 10/21/74 N=1495 4 specimens
(71.2)
"Fertilized" 3/7/74 N=1357 4 specimens
(79.4)
"Embryos" 3/7/74 N=379 1 specimen
(88.4)
"Resting" 3/22/74 N=1894 4 specimens
Percent
0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8
Diameter (mm)

FIGURE 21.—Size composition of oocytes, ova, and larvae within Pacific ocean perch ovaries at different stages of the reproductive cycle. Maturity stage of the gonads these data were collected from is shown above each size frequency curve. Numbers in parentheses indicate the percentage of oocytes that are 0.15 mm or smaller.

passed the fertilization stage. There was no single dominant mode of mature eggs or larvae in any of the fertilized specimens that were examined (Table 15).

Despite the wide range of egg size and development within fertilized specimens, most of their progeny will probably hatch and be released at about the same time. Field observations (Gunderson 1974) indicate that most embryos are released during a single spawning peak that lasts only 2 or 3 wk.

TABLE 15.—Oocyte size frequencies for individual specimens of "fertilized" Pacific ocean perch females.

Oocyte size class (mm)	Number observed				Oocyte size class (mm)	Number observed			
<0.159	262	237	240	227	0.789-0.833	4	1	—	—
0.159-0.203	30	30	26	54	0.834-0.878	—	1	—	—
0.204-0.248	13	10	7	10	0.879-0.923	11	2	1	2
0.249-0.293	5	6	4	7	0.924-0.968	4	—	2	—
0.294-0.338	19	5	3	1	0.969-1.013	4	2	1	—
0.339-0.383	6	1	1	—	1.014-1.058	2	4	10	3
0.384-0.428	1	1	—	—	1.059-1.103	2	4	4	—
0.429-0.473	7	2	1	6	1.104-1.148	1	2	5	1
0.474-0.518	1	—	—	1	1.149-1.193	—	2	2	2
0.519-0.563	3	—	—	2	1.194-1.238	—	5	6	—
0.564-0.608	1	2	2	7	1.239-1.283	—	—	1	—
0.609-0.653	—	—	—	1	1.284-1.328	—	—	—	—
0.654-0.698	2	—	—	—	1.329-1.373	—	2	1	—
0.699-0.743	2	1	—	—	Total	395	321	317	324
0.744-0.788	15	1	—	—					

In view of the oocyte measurement results and the fact that studies on the fecundity of *Sebastes marinus* have suggested a strong element of failure in oocyte fertilization (Raitt and Hall 1967), it seems that current estimates of fecundity must be regarded as somewhat tentative. Complex changes in fecundity probably occur after the first brood of oocytes has been fertilized and detailed morphological work will be required to determine their significance.

For purposes of this study, fecundity was estimated from the number of mature oocytes present prior to fertilization. All oocytes less than 0.30 mm in diameter were classified as immature on the basis of preliminary comparisons of oocyte size frequencies for juvenile and adult specimens. The data in Figure 21 suggest that this cutoff point was somewhat high, however, and that many of the oocytes in the 0.25- to 0.30-mm size class eventually mature. Even if all oocytes that were in the 0.249- to 0.293-mm size class during the collection period were actually maturing, the error generated by calling them immature would be less than about 10%.

Counting the Oocytes

Fecundity was estimated through subsampling by volume. The ovarian contents from each fish were removed from the storage solution, passed through a 1.17-mm screen to remove large particles of ovarian tissue that remained, and placed in a large beaker; water was then added until 2,000 ml of oocytes and water had been obtained. The mixture was stirred magnetically until all oocytes were distributed throughout the water column and a 5-ml subsample withdrawn with a pipette. Care was taken to sample all parts of the water column with the pipette. Four to six subsamples were taken in this manner, the exact number depending on the standard deviation of the first four subsamples.

The oocytes in each subsample were then counted, using a binocular microscope. Two or three replicate counts of each subsample were made by two different observers during the early phases of the study. The number of replicate counts was gradually reduced, however, as it became clear that there was little variation between them. Throughout the study, all counts for a given

fish were partitioned between two different observers to balance out the effects of any bias.

The mean number of eggs per milliliter was calculated for each of the 4-6 subsample means from a given specimen and the coefficient of variation (CV = standard deviation/mean of subsample counts) for these subsample means had the following distribution:

Range of CV *(%)*	*Washington-Oregon*	*QCS*	*Total*
0.0- 4.9	5	4	9
5.0- 9.9	10	16	26
10.0-14.9	17	12	29
15.0-19.9	4	7	11
20.0-24.9	3	1	4
Total	39	40	79

For most specimens (81%), the standard deviation of the subsample means was within 15% of the grand mean. The fecundity of each specimen was estimated by using the formula: $F = 2{,}000n$, where F = fecundity and n = mean number of eggs per milliliter in the subsamples.

Results of Fecundity Study

May (1967) reviewed the results of fecundity work on several species (cod, *Gadus morhua;* herring, *Clupea harengus pallasi;* long rough dab, *Hippoglossoides platessoides*), which showed that, for most practical purposes, variation in fecundity is adequately explained in terms of length alone. Raitt and Hall (1967) came to the same conclusion in their work on the Atlantic redfish, *Sebastes marinus,* a species belonging to the same genus as Pacific ocean perch. They carried out multiple regression of $\log F$ and $\log L$ using weight or age as second independent variables, and it was found that inclusion of variates other than length did not significantly reduce residual variation. As a result, the fecundity work in the current study was directed primarily toward determining the relation between fecundity and length.

Fecundity data for *Sebastes alutus* seemed to fit the relation $F = aL^b$, where F = number of oocytes in thousands, L = fork length in centimeters, and a and b = constants.

The values of a and b were determined by transforming this equation into: $\log F = \log a + b \log L$ and using linear regression techniques to fit $\log F - \log L$ data to a straight line. Data from Washington-Oregon and Queen Charlotte Sound were treated separately, and the following results were obtained:

$$\text{Washington-Oregon}$$
$$F = (0.19295 \times 10^{-9})\, L^{7.32506}$$
$$\text{Queen Charlotte Sound}$$
$$F = (0.12240 \times 10^{-6})\, L^{5.51258}$$

Predicted fecundity at each length was calculated from these relationships, and is shown in Figure 22. The significance of between-area differences in the length-fecundity relation was examined statistically, using the BMD 3R4V[4] computer program for analysis of covariance. The results of this analysis showed that between-area differences in the fecundity-length relation are statistically significant at the 95% level and that they are due to differences in the intercepts of the $\log F - \log L$ regression lines ($F = 5.85$ with 1,76 df) rather than to differences in their slope ($F = 3.43$ with 1,75 df).

Two workers (Westrheim 1958; Snytko 1971) have previously examined the length-fecundity relation for Pacific ocean perch off Washington-Oregon, although neither carried out corresponding studies for the Queen Charlotte Sound stock. Westrheim's results were the first available and were based on examination of 13 specimens. Westrheim collected his fecundity samples during September-November (1951 and 1952), estimated

[4]BMD 3RV. Regression with Analysis of Covariance. This is an addition to the University of California BMD program series, developed at the University of Washington Computer Center by W. Farr.

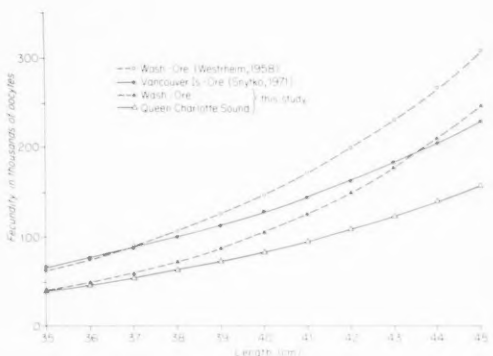

FIGURE 22.—Relation between fecundity and length for Pacific ocean perch off Washington-Oregon (as determined by three different workers) and in Queen Charlotte Sound.

fecundity by a gravimetric method, and found that his results could be represented by the relation: $F = (4.8556 \times 10^{-15})L^{6.33454}$, where L = fork length in millimeters.

Snytko's (1971) fecundity observations on 171 specimens were the most extensive made to date in the Washington-Oregon region. Snytko collected his fecundity samples during November-March 1967-68, in the "Vancouver-Oregon region" (lat. 40°-50°N). The ovaries were collected before fertilization of the oocytes had occurred and fecundity was determined gravimetrically by counting the oocytes present in 0.5- to 1.0-g subsamples of the ovaries (Snytko and Borets 1972). Snytko (1971) presented his data in terms of mean fecundity at a given length and regression of log F on log L indicates that they can be represented by the relation: $F = (0.13103 \times 10^{-5})L^{4.98838}$, where L = length in centimeters.

Length-fecundity relationships for Pacific ocean perch off Washington-Oregon, as predicted by Westrheim (1958), Snytko (1971), and myself are shown in Figure 22. There was substantial variation in the results obtained by different workers and this is to be expected in view of the differences in the timing of ovary collection, techniques used to subsample and count oocytes, and the wide expanse of time (1951-73) covered by the studies. There is also a strong possibility that length-fecundity differences exist between substocks within the Washington-Oregon region and could have contributed to these differences.

The variability in the results of different workers reflects only the difficulties in estimating the number of maturing oocytes a given fish will produce and leaves a larger question unanswered. What we would really like to estimate is the number of viable larvae that fish of a given length or age will give birth to during the embryo-release period, and yet we are totally ignorant of the relationship between the estimated number of maturing oocytes and the number of larvae that will result from them.

Preliminary estimates of the number of larvae that will be released at each age can be made, however, if it is assumed that all oocytes present immediately after fertilization will develop into viable larvae. It should be kept in mind that even though this assumption is patently false, the resulting estimates are still well-suited to between-area comparisons if oocyte-larval mortality does not differ between areas.

It will be recalled that fecundity observations applied to fish collected during August-September, while estimates of mean length at each age applied to the September-December period for Queen Charlotte Sound and to July in the case of the WVI stock. The estimate of the number of larvae released during March of any given year of life (Table 17) was consequently obtained by combining the age-length and length-fecundity relationships pertaining to the previous July-December. For example, the estimated number of larvae released by 11-yr-olds in Queen Charlotte Sound was estimated from predicted mean length at age 10 (Table 3), and the length-fecundity relationship appropriate to that stock ($F = 0.12240 \times 10^{-6} L^{5.51258}$).

RESPONSE OF PACIFIC OCEAN PERCH STOCKS TO FISHING

Methods Used to Examine the Effects of Fishing

In the past, management recommendations for Pacific ocean perch in the INPFC Vancouver area have been developed by arriving at some estimate of the fishing mortality (F) that the stock can withstand, then applying this value to the best available estimate of stock biomass to arrive at a quota. Much discussion has consequently focused on what levels of F can be sustained.

In this section, the effects of different levels of fishing intensity on a hypothetical cohort of fish will be examined, with an approach similar to the yield per recruit analysis that is commonly used in stock assessment. In contrast to conventional yield per recruit analysis, however, I have attempted to look at the costs involved in exerting high levels of fishing intensity on a population, as well as the benefits of increased yield. In particular, the decline in exploitable biomass (CPUE/q, where q is the catchability coefficient) and population fecundity that go hand in hand with increases in yield have been evaluated quantitatively.

The basic computations used to accomplish this are shown in Table 16. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity (Table 17). The mean weight schedule represents average values for the entire year, while the fecundity schedule applies to the embryo release period at the beginning of the year. Vulnerability and mortality were assumed to be constant throughout the year.

TABLE 16.—Example of computations used to estimate exploitable biomass, yield, and population fecundity for a hypothetical Pacific ocean perch population based on N_0 recruits. Input parameters needed are indicated by asterisks.

Age	M_i* Natural mortality coefficient	V_i* Vulnerability coefficient	s_i Proportion alive at beginning of age i	N_i Number alive at beginning of age i	W_i* Mean weight	B_i Mean biomass	B'_i Mean exploitable biomass	Y_i Yield	m_i* Fecundity	E_i Population fecundity
$0 = t_p$	M_0	V_0	$s_0 = 1$	$N_0\, s_0\ (=N_0)$	W_0	$\frac{N_0W_0}{V_0F + M_0}[1 - \exp -(V_0F+M_0)]$	V_0B_0	FV_0B_0	m_0	N_0m_0
1	M_1	V_1	$s_1 = \exp -(V_0F+M_0)$	$N_0\, s_1$	W_1	$\frac{N_1W_1}{V_1F + M_1}[1 - \exp -(V_1F+M_1)]$	V_1B_1	FV_1B_1	m_1	N_1m_1
2	M_2	V_2	$s_2 = s_1\exp -(V_1F+M_1)$	$N_0\, s_2$	W_2	$\frac{N_2W_2}{V_2F + M_2}[1 - \exp -(V_2F+M_2)]$	V_2B_2	FV_2B_2	m_2	N_2m_2
3	M_3	V_3	$s_3 = s_2\exp -(V_2F+M_2)$	$N_0\, s_3$	W_3	$\frac{N_3W_3}{V_3F + M_3}[1 - \exp -(V_3F+M_3)]$	V_3B_3	FV_3B_3	m_3	N_2m_3
							$\sum V_iB_i = B'$	$\sum Y_i = Y$		$\sum E_i = E$

TABLE 17.—Vital statistics for females from the QCS and WVI stocks of Pacific ocean perch.

Age	Mean length (cm)	Mean weight[1] (g)	Fecundity (thousands)	Proportion vulnerable to fishing[2]
		WVI Stock		
8	31.4	433	12.1	0.10
9	32.9	502	17.8	0.20
10	34.3	573	25.1	0.35
11	35.5	639	34.0	0.52
12	36.6	704	43.7	0.64
13	37.6	766	54.7	0.69
14	38.6	833	66.6	0.75
15	39.4	889	80.8	0.87
16	40.2	947	93.9	1.00
17	41.0	1,008	108.8	1.00
18	41.6	1,056	125.7	1.00
19	42.2	1,105	139.8	1.00
20	42.7	1,147	155.2	1.00
21	43.2	1,190	169.2	1.00
22	43.7	1,234	184.3	1.00
23	44.1	1,270	200.5	1.00
24	44.5	1,307	214.3	1.00
		QCS Stock		
9	34.3	573	—	0.20
10	35.9	662	—	0.31
11	37.2	741	45.7	0.44
12	38.5	826	55.7	0.53
13	39.6	903	67.3	0.62
14	40.6	977	78.6	0.79
15	41.4	1,040	90.1	0.94
16	42.2	1,105	100.4	1.00
17	42.9	1,164	111.5	1.00
18	43.6	1,225	122.1	1.00
19	44.1	1,270	133.5	1.00
20	44.6	1,316	142.2	1.00
21	45.0	1,354	151.3	1.00
22	45.4	1,392	158.9	1.00
23	45.8	1,431	166.9	1.00
24	46.1	1,461	175.2	1.00

[1]Estimated from the age-length data in Table 3 and Westrheim and Thomson's (1971) all-B.C. length-weight relation for females: $W = 0.0078571\, L^{3.16734}$.

[2]Vulnerability coefficients for 8- and 9-yr-olds were assigned arbitrarily. The values used were more conservative than those predicted by extrapolation of the straight line obtained for 10- to 16-yr-olds (0.20 for 8-yr-olds and 0.29 for 9-yr-olds).

Yield, exploitable biomass, and total fecundity are calculated for each age group, then summed. The results give the annual yield to the fishery, annual production of larvae, and average exploitable biomass on hand during the year for an equilibrium population of Pacific ocean perch. This population is based on a constant number of recruits (N_0), with individual growth and mortality being determined by the input values of the constants used to describe mortality, vulnerability to fishing, and mean weight at each age.

A computer program[5] was written to carry out the calculations in Table 16 and offers a variety of ways to evaluate the effects of different fishing strategies on a stock. The basic calculations can be carried out for any combination of instantaneous rates of fishing mortality (F) and age of entry into the fishery (t'_p) that the user specifies.

The mesh size used when fishing for Pacific ocean perch is dictated primarily by convenience, since the incidence of "gilling" and entanglement in the meshes is reduced sharply when using 3.0-inch mesh (internal measure) in the cod end. This was not found to be the case in mesh studies with Atlantic redfish (Templeman 1963), where use of smaller cod end mesh sizes simply "gilled" fish of a smaller size. In the Pacific ocean perch stocks examined in this paper, recruitment to the fishing grounds is quite gradual and the fish that would normally be "gilled" in a 3.0-inch cod end are poorly represented on the grounds.

Pacific ocean perch offer a special case then, where evaluation of the effects of different size or age restrictions is of no practical interest for fisheries management. Consequently, all analysis in this section was focused on determining the optimal intensity of fishing for the Pacific ocean

[5]D. Gunderson and J. Buss. 1976. Users guide to ASSESS: Assessment of the effects of different fishing strategies on fish populations (FORTRAN IV). Norfish Pap. NC09, 8 p.

perch stocks being examined and the effects of varying the age at entry into the fishery (t'_p) were ignored.

In addition, the analysis was restricted to the female portion of the stock. Over the long term, the population will be far more sensitive to removals of females and reduced population fecundity than it will to removals of males, and the optimal harvest rate for females will determine the level of F that should be applied to the stock as a whole.

The input data used to describe the QCS and WVI stocks are shown in Table 17. The values used for mean weight at age, vulnerability coefficients, and fecundity at age were derived from the information in Tables 3 and 6 and Figure 22. Natural mortality was assumed to be the same for all age groups concerned and computations were carried out for both $M = 0.1$ and $M = 0.2$.

Assessment of Immediate Response to Fishing

Only a small fraction of fish less than 8 yr old are recruited to the fishing grounds and, for the purposes of this study, it was assumed that recruitment begins at age 9 ($t_p = 9$). It is possible that significant quantities of 9-yr-olds are discarded by fishermen, however, making it difficult to estimate their vulnerability coefficient from market samples. For this reason, $t_p = 10$ was also considered, so that the sensitivity of the results to changes in t_p could be evaluated.

The results (Figure 23) showed that different values of t_p had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing F. In fact, the relative levels of each followed almost identical trends for both stocks and both values of t_p considered. However, the value of M used in the calculations had a pronounced effect on the results.

In all cases examined, there was a sharp rise in yield as F increased from 0.0 to 0.2, and a more gradual increase for F-values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as F increased from 0.0 to 0.2, then declining more gradually for F greater than 0.2.

Relative changes in population fecundity were almost identical to changes in exploitable biomass, indicating that changes in CPUE can be used directly to estimate the magnitude of changes in population fecundity. During 1966-68, then, population fecundity for stocks in the Oregon-Queen Charlotte Sound region must have declined in the same manner as CPUE and is currently only about 50% of what it was prior to intensive fishing.

Preliminary examination of the data (Figure 23) shows that the most significant changes in yield, exploitable biomass, and population fecun-

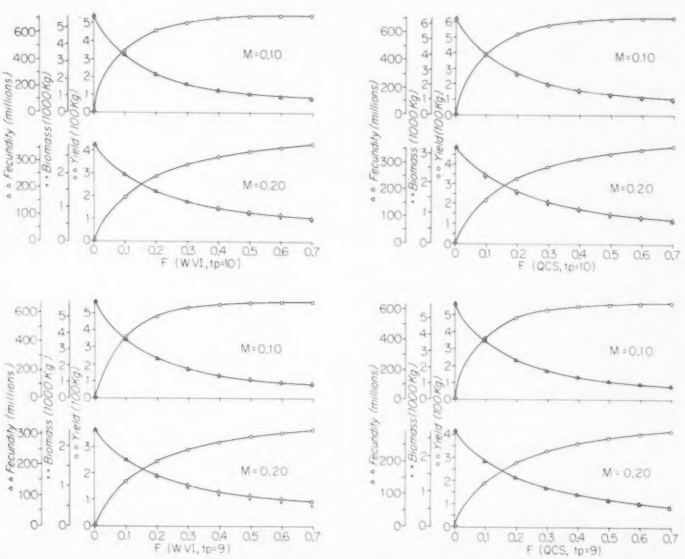

FIGURE 23.—Population fecundity (estimated number of larvae released annually), exploitable biomass, and annual yield for hypothetical populations based on 1,000 recruits per year. Results are presented by stock, for two different ages at recruitment (t_p) and two different levels of instantaneous natural mortality (M).

TABLE 18.—Relative yield (Y/Y_{max}), population fecundity (E/E_{max}), and exploitable biomass (B'/B'_{max}) at $F = 0.1$ and 0.2.[1] The range of values obtained by taking $t_p = 9$ or 10, for two different stocks of Pacific ocean perch is presented.

Item	$F = 0.1$		$F = 0.2$	
	$M = 0.1$	$M = 0.2$	$M = 0.1$	$M = 0.2$
Y/Y_{max}	0.62-0.64	0.45	0.84-0.85	0.67
E/E_{max}	0.59-0.62	0.68-0.70	0.40-0.43	0.51-0.53
B'/B'_{max}	0.60-0.61	0.68	0.40-0.41	0.50-0.51

[1] Y_{max} = yield when $F = 0.7$; E_{max} and B'_{max} = population fecundity and exploitable biomass when $F = 0.0$.

dity occurred when $F = 0.1$ and $F = 0.2$, and the results for these two levels of fishing intensity have been summarized in Table 18. All data were presented in terms of the range of values obtained when considering different stocks and t_p values. The ranges were always quite narrow, attesting to the fact that consideration of different stocks and t_p values had little influence on the results.

The conclusions that can be drawn from Table 18 depend to a large degree on what is considered to be the best estimate of M. If $M = 0.1$, the costs of letting F reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. From this consideration alone, it would seem advisable to limit F to 0.1.

If $M = 0.2$, however, the costs of letting F reach 0.2 are somewhat lower with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock. Limiting F to 0.1 would reduce the yield to only 45% of the level attainable at $F = 0.7$, while population fecundity and exploitable biomass would undergo reductions of about 30% from virgin stock levels.

On the basis of this analysis, then, there is a reasonable possibility that if $M = 0.2$, the optimal level of F could be as high as 0.2. From a biological point of view, however, a central question still remains unanswered, since we have not yet evaluated the consequences of reducing population fecundity. It is one thing to point out the degree to which population fecundity will be reduced by various levels of fishing intensity and quite another to determine the impact this reduction will have on future recruitment.

Effects of Fishing on Future Recruitment

Variability in egg and larval survival is extremely high for marine teleosts. Larvae grow rapidly during the planktonic phase and require large quantities of food. For example, haddock larvae initially grow at rates of about 12% per day, increasing in weight by a factor of 10^5 during their first year of life (Jones 1973). When food is not plentiful, available supplies can be exhausted rapidly, resulting in starvation and high rates of density-dependent mortality. Even if larval mortality is not directly due to starvation, density-dependent mortality could easily result from slow growth and prolonged exposure to predators (Cushing 1974).

Density-independent mortality, such as that suffered when eggs or larvae are swept into unfavorable nursery areas, can also be quite variable. Ketchen (1956) and Ketchen and Forrester (1966) found that in the case of English sole and petrale sole, mortality of this nature seems to account for a high proportion of the variability in year class strength.

Marine fish have evolved three basic ways of adapting their life history to cope with the highly variable survival of their progeny: 1) iteroparity (repeat spawning), 2) high fecundity, and 3) complete elimination of the egg and/or larval stage through ovoviviparity or viviparity. Murphy (1968) has shown that iteroparity is favored under conditions of high variability in larval survival and relatively constant adult mortality. This line of evolution leads to the existence of a large number of adult age-groups—a common situation in marine fishes. With several adult age-groups in the population, the size of the adult stock is buffered somewhat against variations in the strength of individual year classes.

High fecundity and elimination of the planktonic phase offer two divergent means of coping with variable larval mortality and are typified best by the gadoids on one hand and by elasmobranchs on the other. Atlantic cod commonly produce several million eggs per adult, and Cushing and Harris (1973) have shown that the spawner-recruit relation for this species is distinctly convex or dome-shaped (curve a in Figure 24). This relationship implies that eggs are "overproduced" at high parental stock densities, with attendant declines in larval survival. At stock densities below the replacement point (P_r), the high fecundity allows for great resilience and rapid return to P_r.

The development of most elasmobranchs is characterized by the elimination of the larval stage found in the majority of teleosts and the young are fully developed when born. Fecundity is extremely low, with 2-108 young being produced

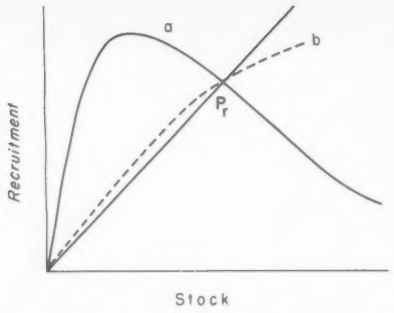

FIGURE 24.—Relationship between parent stock and recruitment for gadoids (a) and elasmobranchs (b).

per year (Holden 1973). Any compensatory responses to increase the number of recruits must act through changes in growth (with attendant changes in the age at maturity) or fecundity, and are relatively sluggish. Holden (1973) has suggested that the stock-recruitment relation for most elasmobranchs is probably of the form of curve b in Figure 24, departing little from the bisector on either side of the replacement point.

By eliminating the free-living larval stage, elasmobranchs have reduced the susceptibility of adult stock size to environmental perturbations. In the natural state, then, the compensatory mechanisms that return the stock to P_r do not need to provide the same degree of resilience they do in the gadoids. This lack of resilience makes the elasmobranchs poorly adapted to harvests by man, however, and they are quite susceptible to overfishing.

Pacific ocean perch are ovoviviparous, and, like the elasmobranchs, they are probably much less resilient to perturbations from P_r than a highly fecund, oviparous species like cod. It is important, therefore, that population fecundity be kept quite near the levels found in the virgin stock when the adult stock was presumably near P_r. Any reduction in population fecundity from virgin stock levels could easily result in reduced recruitment.

Some increases in the number of larvae released could probably come through compensatory growth, since the age at sexual maturity and level of individual fecundity are both correlated strongly with size. There must be some limits to the degree of compensation this mechanism is capable of, however, and this was explored quantitatively by using the model (Table 16) and computer program described previously.

This analysis was begun by setting up four sets of hypothetical populations (one set for each stock) and calculating the population fecundity under different levels of fishing mortality. In the first population, the "standard" age-length data in Table 17 were used to describe individual growth in each stock. In the second and third populations, the mean lengths at each age were increased 3% and 5% (Figure 25) to simulate compensatory growth. In the fourth population, mean length at each age was again increased 5% above standard, and it was also assumed that sexual maturation occurred 1 yr earlier than in the other populations. The latter assumption was justified by the fact that a 5% increase in growth brought 8-yr-olds from the WVI stock and 10-yr-olds from the QCS stock up to the size at which sexual maturity occurred in the standard population (Figure 25). The last population was presumed to embody the maximum possible degree of compensation in population fecundity, since the projected increases in mean length at age would be quite remarkable in a species growing as slowly as *S. alutus*. The assumption that the age at sexual maturity would decline because of earlier attainment of a critical maturation size is also tenuous, and only time will tell if this actually occurs.

The age of recruitment was taken as age 8 for the WVI stocks and age 10 for the QCS stocks, in

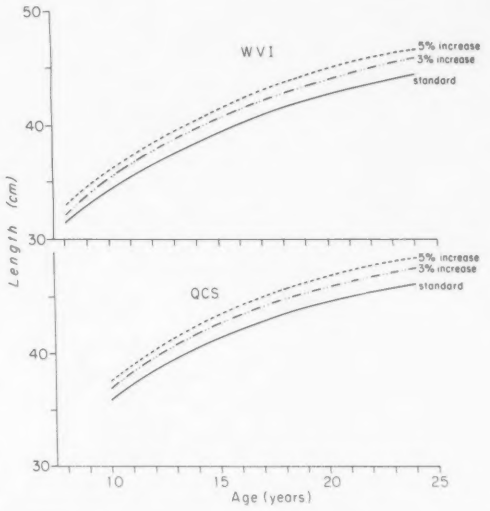

FIGURE 25.—Mean length at age for female Pacific ocean perch in the WVI and QCS stocks, assuming standard growth, and two different levels of compensatory increase in growth.

TABLE 19.—Estimated population fecundity (millions of larvae released) for hypothetical Pacific ocean perch populations based on 1,000 recruits per year, under different levels of fishing mortality and compensatory growth and maturity.

	WVI stock				QCS stock		
	F				*F*		
Item	0.0	0.1	0.2	Item	0.0	0.1	0.2
				M = 0.1			
Standard growth, mature at age 9	607	356	237	Standard growth, mature at age 11	703	437	302
3% increase, mature at age 9	753	442	294	3% increase, mature at age 11	828	515	356
5% increase, mature at age 9	867	510	339	5% increase, mature at age 11	920	572	396
5% increase, mature at age 8	884	527	357	5% increase, mature at age 10	966	618	442
				M = 0.2			
Standard growth, mature at age 9	256	174	130	Standard growth, mature at age 11	358	251	191
3% increase, mature at age 9	318	216	162	3% increase, mature at age 11	422	296	225
5% increase, mature at age 9	366	249	187	5% increase, mature at age 11	469	328	249
5% increase, mature at age 8	383	266	204	5% increase, mature at age 10	515	375	296

order to accommodate the changes in age at maturity. It was assumed that the length-weight relationships, length-fecundity relationships, and vulnerability coefficients characterizing the standard populations would apply to the other populations as well. All calculations have been carried out for $M = 0.1$ and $M = 0.2$.

The results (Table 19) for standard growth when $F = 0$ give the estimated population fecundity for the virgin stock. In actual fact, biomass was reduced below virgin stock levels several years prior to the time when the "standard" rates of growth were estimated and some compensatory changes could already have occurred. The population fecundity in the "standard" population when $F = 0$ could consequently overestimate preexploitation fecundity to some degree.

For both stocks considered, fishing mortalties greater than $F = 0.1$ doom Pacific ocean perch to lower levels of population fecundity than those existing prior to exploitation. None of the populations examined were able to recover preexploitation levels of population fecundity when $F = 0.2$, even when mean length at age increased by 5% and sexual maturation occurred a year earlier than normal.

Even if F is restricted to 0.1, the ability to regain virgin stock levels of fecundity varies sharply with M. If $F = M = 0.1$, the results for both stocks show that even if growth increases by 5% and sexual maturation occurs a year earlier than normal, population fecundity will be 12-13% less than in the virgin stock. If $M = 0.2$, the outlook is better, since the stocks were able to recover 92-97% of the preexploitation fecundity with a 5% increase in growth.

The main point to be considered, however, is that even when $F = 0.1$, Pacific ocean perch would have to undergo significant compensatory changes in growth to regain virgin stock levels of population fecundity and would possibly have to mature a full year earlier than normal. In this light, the intensive fishing of the U.S.S.R. and Japanese trawl fleets in the past has been quite remote from the concept of long-term equilibrium yield.

In the case of the WVI stock, exploitation was most intensive during 1967, and, depending on the value of M used, 1967-68 estimates of F ($= Z - M$) would range from 0.36 to 0.46 (Figure 17). In almost every year since, the estimated value of F would exceed 0.1, regardless of whether $M = 0.1$ or 0.2. The situation is less clear in the case of the QCS stock, but mortality estimates based on the age composition of the Washington trawl fleet (Figure 16) indicate that F was between 0.66 and 0.76 during 1968-69 and exceeded 0.1 during 1969-72.

Drastic action will probably be required to return Pacific ocean perch to their former levels of population fecundity, beginning perhaps with a total ban on commercial fishing, such as that proposed by Snytko (1971). Once this has been accomplished, harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed 0.1 $\hat{\beta}$, where $\hat{\beta}$ is the estimated stock biomass.

SUMMARY

Pacific ocean perch are a dominant component of the fauna of the North Pacific, attaining a wide geographic distribution and high levels of population density prior to exploitation. Intensive exploitation by man created a sudden change in their population biology, and one that they were poorly adapted to cope with. Pacific ocean perch stocks lack the resilience of highly fecund, oviparous groups like the gadoids and their ability to main-

tain even current levels of abundance is uncertain.

The biology and population dynamics of Pacific ocean perch in the Washington-Queen Charlotte Sound region were examined in detail, to gain some insight into the effects of different fishing strategies on this species. Two stocks were delineated: one in Queen Charlotte Sound (QCS stock) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI stock).

Production in the region occupied by the WVI stock plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period. The QCS stock was affected less drastically by fishing, since biomass estimates and CPUE data indicated that *S. alutus* were initially more abundant in the former area and did not undergo such intensive exploitation. During 1966-68, production declined 50%, while CPUE of Washington trawlers declined 36%.

Changes in size and age composition of Pacific ocean perch in the commercial landings were examined for the years 1967-73. Substantial quantities of large *S. alutus* were present in Queen Charlotte Sound during 1956-58 and subsequent changes in size and age composition reflected the changes caused by commercial fishing and recruitment of two strong series of year classes. The first series was centered around the 1952 year class and included the 1951-53 brood years, while the second series centered around the 1961 and 1962 brood years. Size composition data for the WVI stock were too limited to be useful prior to 1961, but data for subsequent years suggested that the same year classes that predominated in Queen Charlotte Sound were also predominant in landings from the WVI stock.

Fisheries exploitation has resulted in drastic reductions in the abundance of the 1951-53 year class series in both the QCS and WVI stocks and the 1973 Washington trawl catches from these stocks were dominated by 10- to 13-yr-old fish.

Growth rates were estimated from commercial fisheries and research cruise data, taking pertinent features of the life history such as seasonal and bathymetric variability in the age-length relation into consideration. Parameters of the von Bertalanffy growth model were estimated by sex for both the QCS and WVI stocks.

Although fish older than age 10 are large enough that almost all can be caught by conventional trawling gear and retained for market sales, age composition data from commercial catches and research surveys showed that recruitment to the fishing grounds is not complete until much later than age 10. The proportion of each age group vulnerable to fishing (V_i) was estimated by employing a model that assumed that natural mortality (M) and V_i were constant throughout the year. The results suggested that recruitment to the fishing grounds differed somewhat between stocks, but that V_i ranged from 0.31-0.35 during age 10 to 0.87-0.94 during age 15. Estimation of V_i could not be made for fish less than 10 yr old, since these age groups may be subject to substantial rates of discard by fishermen.

Any yield per recruit analysis of Pacific ocean perch stocks must take these recruitment patterns into consideration to be meaningful. Recruitment to the fishing grounds is quite gradual, and many age groups that could potentially be retained by conventional mesh sizes are poorly represented on the fishing grounds. Evaluation of the effects of different size or age restrictions would be quite misleading if this were not considered.

Age composition data (number caught per hour by age-group) were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year n to ages 15-19 in year $n + 1$, or to ages 16-20 in year $n + 2$. These survival estimates were then converted to total instantaneous mortality rates (Z) and plotted against total international effort ($\bar{f}$) on the assumption that they conform to the model: $Z = q\bar{f} + M$, where M = instantaneous natural mortality rate. The data seemed to fit this model in a general way but there was a relatively low correlation between Z and $\bar{f}$ (r = 0.3-0.5), due principally to wide variability in the availability of Pacific ocean perch to on-bottom trawls (totally unrelated to variations in actual abundance) and to the low quality of the data on international fishing effort. Despite this, there was good agreement between the estimates of M derived from this study (0.07 for the QCS stock and 0.23 for the WVI stock) and results obtained in previous studies. It was concluded that between-stock differences in natural mortality probably should not be overemphasized, and that the results of the mortality studies served mainly to show that M in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

Data on the proportion of sexually mature individuals in each age-length group were sum-

marized by stock and suggested that maturation of both male and female Pacific ocean perch depends more on the size of a fish than on its age. The maturation length (where 50% of the fish in that length group are sexually mature) showed statistically significant differences between stocks, fish from the WVI stock maturing at a smaller size than those from the QCS stock. Males matured at 29.4 cm in the WVI stock and 30.5 cm in the QCS stock, while corresponding values for females were 34.2 and 36.3 cm.

Estimates of the age at sexual maturation indicated that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. The results for males suggest that males from the WVI stock mate for the first time when 6 yr old, while this occurs at age 7 in the QCS stock.

Measurement of oocyte diameters from a series of ovaries collected over the complete extent of the reproductive cycle suggested that any estimates of fecundity must be regarded as tentative, owing to the uncertain significance of auxiliary modes of oocytes. Incomplete fertilization of oocytes also complicates the situation, and there is very little known about the relation between the number of developing oocytes and the number of viable larvae that will result from them.

Length (L)-fecundity (F) data were summarized by stock and were described by the relation: $F = aL^b$. Analysis of covariance showed that there were significant between-area differences in the length-fecundity relationship, females from Washington-Oregon being more fecund than Queen Charlotte Sound females of comparable length.

The effect of fishing on stocks of Pacific ocean perch was examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment. However, the model and computer program developed for this study differ from conventional methods in that they allow for estimation of exploitable biomass and population fecundity as well as yield per recruit. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity. Annual yield to the fishery, annual production of larvae, and average exploitable biomass on hand during the year were then calculated for a population based on a constant number of female recruits, assuming different combinations of instantaneous fishing mortality (F) and age of recruitment to the fishery (t_p).

The results showed that different levels of t_p, or between-stock differences in the input parameters had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing F. In all cases examined, there was a sharp rise in yield as F increased from 0.0 to 0.2 and a more gradual increase for F-values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as F increased from 0.0 to 0.2, and declining more gradually for F greater than 0.2.

The value of M used in the calculations had a pronounced effect on the results. If $M = 0.1$, the costs of letting F reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. If $M = 0.2$, however, the costs of letting F reach 0.2 are somewhat lower, with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock.

This preliminary analysis provided some estimates of the reductions in population fecundity that could be expected under different levels of fishing intensity, but gave no insight into the effects of this reduced fecundity on future recruitment. As a result, the analysis was carried one step further and it was assumed that, at reduced levels of population density, all compensatory changes in recruitment are mediated through increases in growth. Attendant changes in fecundity at age and age at sexual maturation would then tend to increase the level of population fecundity and recruitment, since both fecundity and maturation are related to size.

Three hypothetical levels of compensatory growth and sexual maturation were considered, and none of these were effective in restoring preexploitation levels of population fecundity when $F = 0.2$. This was true even when mean length at each age increased 5% and sexual maturation occurred a year earlier than normal. Even when F is restricted to 0.1, Pacific ocean perch would have to undergo significant compensatory changes in growth to restore population fecundity to virgin stock levels, when the stock was presumably near the replacement point (P_r) on the spawner-recruit curve.

Since Pacific ocean perch stocks are poorly adapted to extensive displacements from P_r, it was suggested that drastic action will probably be required to return them to their former levels of population fecundity, beginning perhaps with a

ban on fishing. Once the stocks approach their former levels of abundance, the harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed $0.1\hat{\beta}$, where $\hat{\beta}$ is the estimated stock biomass.

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ANALYSIS OF AGE DETERMINATION METHODS FOR YELLOWTAIL ROCKFISH, CANARY ROCKFISH, AND BLACK ROCKFISH OFF OREGON[1]

LAWRENCE D. SIX[2] AND HOWARD F. HORTON[3]

ABSTRACT

Age determination methods and their application are presented for yellowtail rockfish, *Sebastes flavidus;* canary rockfish, *S. pinniger;* and black rockfish, *S. melanops*, collected off Oregon during 1972-75. Of 25 anatomical structures examined, those compared for consistency of readings were the anal fin pterygiophore, opercle, otolith, scale, and vertebra. Various heating, staining, and microscopy techniques were applied to otoliths and scales with little success. The effect of deviation between otolith readings on survival estimates and age-length relationships is discussed. Consistency of otolith readings was generally superior to other structures for these three species. For yellowtail, canary, and black rockfishes, respectively, 71, 76, and 76% of two independent otolith readings deviated by no more than ±1 assumed annulus. Consistency of otolith readings for all three species decreased with age. Even though age estimates were not completely consistent, Chapman-Robson and catch curve estimates of survival, as well as age-length relationships, each derived from two readings of the same set of otoliths, were not significantly different at the 95% level for the three species. Age-length relationships are given for both male and female yellowtail, canary, and black rockfishes.

In 1973, yellowtail rockfish, *Sebastes flavidus* (Ayres); canary rockfish, *S. pinniger* (Gill); and black rockfish, *S. melanops* Girard, composed 41, 38, and 4%, respectively, of the total Oregon commercial trawl catch of rockfishes consisting of 19 species (Oregon Department of Fish and Wildlife[4] unpubl. data). Because little is known of the biology of these fishes, information on age, length, and weight are needed for estimates of mortality, growth, and ultimately sustainable yield.

The investigation was based on analysis of samples taken off Oregon from 1972 to 1975. The overall objective was to determine if an acceptable technique(s) could be developed for age determination of these species. Specific objectives were: 1) to determine if counts of annuli on aging structures can be reproduced consistently; and 2) to determine if deviations between successive counts of annuli significantly affect estimates of survival and the age-length relationships.

Considerable effort has been expended on age determination of commercially important species of *Sebastes* in the North Atlantic. Perlmutter and Clarke (1949) used scales to age juvenile redfish, *S. marinus*, but did not include older fish in the study because of difficulty in discerning annuli. Kelly and Wolf (1959) reported 100% agreement between independent readings of redfish otoliths with less than 10 annuli, but agreement between readings for fish from 7 to 20 + yr was only 31%. Sandeman (1961) used scales for juvenile redfish (<5 yr), but found otoliths to be superior for older fish.

In the North Pacific Ocean, the majority of research relative to our study has been conducted on the Pacific ocean perch, *S. alutus*. Alverson and Westrheim (1961) reported readability of scales for Pacific ocean perch was only fair, while Chikuni and Wakabayashi (1970) were satisfied with scales for the same species. Westrheim (1973) subsequently found that agreement between readings of Pacific ocean perch otoliths decreased from 100% for 0-zone otoliths to 26% for 19-zone otoliths. Phillips (1964) found both scales and otoliths could be used for valid age estimations for 10 species of California rockfish, includ-

[1]Supported by funds from the Oregon Department of Fish and Wildlife. Technical Paper No. 4254, Oregon Agricultural Experiment Station, Corvallis, OR 97331.

[2]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; present address: Pacific Marine Fisheries Commission, 1400 SW. Fifth Avenue, Portland, OR 97201.

[3]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.

[4]Formerly known in part as the Fish Commission of Oregon.

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ing *S. flavidus* and *S. pinniger*, but used scales because they were obtained with less effort. Miller and Geibel (1973) preferred scales to otoliths for blue rockfish, *S. mystinus*, off California because scales allowed greater ease in back-calculation of growth. Wales (1952), working on the same species, reported that scales were easier to read than otoliths. Chen (1971) found scales were frequently regenerated on rockfish of the subgenus *Sebastomus*, so he used otoliths for age determination.

Otoliths were used to age copper rockfish, *S. caurinus*, in Puget Sound (Patten 1973) and northern rockfish, *S. polyspinis*, in the Gulf of Alaska (Westrheim and Tsuyuki 1971). There are no published reports on the life of *S. melanops*, although Miller (1961) indicated that the ages of several specimens were estimated. Westrheim and Harling (1975) used otoliths to determine age-length relationships for 26 scorpaenids in the northeast Pacific.

TABLE 1.—Structures examined from yellowtail rockfish, canary rockfish, and black rockfish with a description of their suitability for age determination.

Structure	Description
Anal fin pterygiophore	enumerable zones present
Anal spine	zones present, but not enumerable
Articular	insufficient calcification
Asteriscus	insufficient calcification
Basipterygium	zones present, but not enumerable
Ceratohyal	insufficient calcification
Cleithrum	zones present, but not enumerable
Dentary	zones present, but not enumerable
Epihyal	insufficient calcification
Hypurals	insufficient calcification
Interopercle	zones present, but not enumerable
Lachrymal	insufficient calcification
Lapillus	insufficient calcification
Maxilla	zones present, but not enumerable
Mesopterygoid	insufficient calcification
Neurocranial bones	insufficient calcification
Opercle	enumerable zones present
Pelvic fin rays	zones present, but not enumerable
Postcleithrum	insufficient calcification
Premaxilla	zones present, but not enumerable
Sagitta	enumerable zones present
Scale	enumerable zones present
Subopercle	insufficient calcification
Supracleithrum	zones present, but not enumerable
Vertebral centrum	enumerable zones present

METHODS AND MATERIALS

Most fish used in this study were sampled randomly from the commercial trawl landings in Astoria and Coos Bay, Oreg., from 1972 to 1975. Sex, length to the nearest centimeter, and weight to the nearest gram were recorded, and one or both saccular otoliths (sagittae) were extracted. Twenty-five anatomical structures (Table 1), including the anal fin pterygiophores (largest), opercles, otoliths, scales, and several anterior vertebrae were sampled from carcasses obtained from fish processing plants in Newport, Oreg., from 1974 to 1975. Juvenile fish were collected on research cruises on the Oregon continental shelf from 1972 to 1974, and by scuba and hook-and-line in Yaquina and Tillamook bays from 1973 to 1975.

Otoliths were stored in a 50:50 solution of glycerine and water and read using reflected light on a dark background utilizing a binocular dissecting microscope at 10×. Otolith sections 0.3 mm thick were obtained with a thin sectioning machine after being embedded in polyester casting resin. Scales were cleaned, dried, and mounted between glass slides or impressed on acetate cards and read using a scale projector with a 48-mm objective. Other structures, including opercles, pterygiophores, and vertebrae were heated in a detergent-water solution at 50°C for 20 min to remove adhering tissue and air dried. Opercles were examined with the naked eye and pterygiophores and vertebrae were examined by use of a binocular dissecting microscope at 10×.

One year of the life of the fish was assumed to be represented by an opaque zone followed by a hyaline zone on otoliths (Kelly and Wolf 1959; Westrheim 1973) as well as on opercles, pterygiophores, and vertebrae. A scale annulus was defined as a zone of closely spaced circuli (check) following a zone of widely spaced circuli (Van Oosten 1929; Tesch 1968). True annuli are represented by pronounced hyaline zones on otoliths and bony structures and by pronounced checks on scales. Indistinct zones or zones that are split or discontinuous were considered accessory (false) annuli. A zone that obviously interrupts the periodicity of the pattern of zonation was considered to be accessory unless it occurred in many fish in the same sample.

Consistency of readings of aging structures was measured by the ability of the reader to reproduce successive, independent counts of annuli. To insure independence there was a period of several months between most otolith readings. When the period was less than 2 wk, a five digit code number was assigned to each structure to prevent possible memorization of previous age estimations. Independent readings of yellowtail rockfish otoliths were made by two people, while those of canary and black rockfishes were made by the same person.

Age composition data were described graphically by FISHPLOT, a computer plotting routine based on the method of Hubbs and Hubbs (1953). Survival estimates were obtained by the Chapman-Robson (Robson and Chapman 1961) and the catch curve (Ricker 1975) methods. The age-length relationship of yellowtail rockfish was described by the equation $L = cA^b$, where L = length (centimeters), A = estimated age (years), and c and b are constants. The age-length relationships for canary and black rockfish were described by the von Bertalanffy growth-in-length equation with the computer program BGC-2 (Abramson 1965) using the method of least squares weighted according to sample size (Tomlinson and Abramson 1961).

A total of 71 young unsexed black rockfish, mostly young-of-the-year, were used in the age-length analysis. Their corresponding lengths were applied to both males and females, with the assumption that there were little or no sexual differences in length at these younger ages. The assumption was based on the fact that growth curves for male and female Pacific ocean perch, obtained by Westrheim (1973) for fish from Oregon to British Columbia and by Gunderson (1974) for Washington samples, were nearly identical at ages less than 6 yr.

RESULTS AND DISCUSSION

Suitability of Structures for Age Determination

Only 5 of 25 anatomical structures sampled were suitable for estimation of age. These were the anal fin pterygiophore, opercle, otolith, scale, and vertebra. The criterion used to determine suitability for aging was the presence of enumerable growth zones. Based on examination of a limited sample, most structures did not satisfy this criterion because: 1) they were not sufficiently calcified to reveal distinct growth zones, or 2) calcification was evident but growth zones were not discernible (Table 1). The above five structures were examined further to determine whether successive, independent estimates of age were consistent.

Consistency of Readings

Percent agreement between two independent counts (readings) of assumed annuli by the same person on anal fin pterygiophores, opercles, otoliths, scales, and vertebral centra sampled from the same yellowtail, canary, or black rockfish is presented in Table 2. Exact agreement ±1 assumed annulus is also given. Agreement was low for all structures and species except otoliths of canary rockfish. Agreement between otolith readings for yellowtail and canary rockfishes was superior to agreement between readings of other structures, with 71 and 97% agreement ±1 assumed annulus, respectively. For the sample of black rockfish, otoliths and opercles were equally readable with 74 and 75% agreement ±1 assumed annulus, respectively.

Means of the two readings of the five structures agreed fairly well for black rockfish, indicating that counts of assumed annuli on the structures were similar. Means were not similar for these structures from yellowtail and canary rockfishes.

A number of samples of each structure were not read due to crystallization and breakage of otoliths, regeneration of scales, and poor calcification of opercles and pterygiophores. Throughout the entire study at least one of the two otoliths was partially or completely crystallized in 23 of 1,116 (2.1%) yellowtail rockfish, 27 of 666 (4.1%) canary rockfish, and 29 of 302 (9.6%) black rockfish. There were more readable vertebral centra and otoliths than any of the other structures. Many

TABLE 2.—Estimations of age, number of readable structures, and percent agreement of two independent readings of five structures sampled from 35 yellowtail rockfish, canary rockfish, and black rockfish landed off Newport, Oreg., 1974-75.

Structure	Estimated age (yr)		No. readable	Agreement (%)	
	Min-max	Mean		Exact	±1 yr
Yellowtail rockfish					
Anal pterygiophore	9-18	12.5	29	24	59
Opercle	—	—	3	—	—
Otolith	10-18	15.2	34	24	71
Scale	8-15	11.2	32	16	59
Vertebral centrum	8-18	12.9	35	11	49
Canary rockfish					
Anal pterygiophore	7-20	9.5	33	33	76
Opercle	4-18	7.8	31	10	48
Otolith	5-22	8.9	35	77	97
Scale	7-23	10.7	32	31	69
Vertebral centrum	5-18	8.9	35	31	60
Black rockfish					
Anal pterygiophore	5-18	9.6	32	19	66
Opercle	5-18	9.2	28	39	75
Otolith	6-15	10.7	35	40	74
Scale	7-16	10.7	31	23	61
Vertebral centrum	6-18	10.3	35	14	54

opercles were not readable, especially those sampled from yellowtail rockfish, where 32 of 35 could not be used for age determination.

Consistency of otolith and scale readings subsequently was compared in a larger sample. A chi-square test for paired data corrected for continuity revealed that exact agreement between otolith readings was significantly greater than exact agreement between scale readings for yellowtail ($P<0.05$)[5] and black ($P<0.005$) rockfishes (Table 3). No significant difference occurred between readings of otoliths and scales for canary rockfish ($P>0.90$). Percent agreement between first readings of both structures for all three species was low.

TABLE 3.—Percent agreement in estimates of age between first and second readings of the same structure and between first readings of different structures (otoliths and scales) sampled from the same yellowtail rockfish, canary rockfish, or black rockfish caught off Oregon, 1974-75.

	Within structures						
	Otolith		Scale		Between structures		
Species	Exact	±1	Exact	±1	Exact	±1	*N*
Yellowtail rockfish	42	80	26	60	14	53	89
Canary rockfish	37	73	36	70	15	39	91
Black rockfish	48	81	26	54	11	43	98

In terms of consistency of readings, the otolith is the best structure of those examined for age determination of yellowtail, canary, and black rockfishes; yet, even this method is questionable. Deviations of readings of yellowtail rockfish otoliths by two readers generally increased with age of the fish (Figure 1). For canary rockfish otoliths read twice by the same person, deviations of readings initially increased and then stabilized with increasing age (Figure 2). Deviations of readings of black rockfish otoliths read twice by the same person also increased with age of the fish (Figure 3). The distribution of deviations is skewed considerably in the positive direction, indicating that the second reading was substantially lower than the first. For our largest sample of 322 yellowtail rockfish, 481 canary rockfish, and 357 black rockfish, respectively, 71, 76, and 76% of the two readings deviated by no more than ±1 assumed annulus. In a study on Pacific ocean perch by Westrheim (1973), 85% of two otolith readings by different people deviated by no more

[5]Probability of a greater chi-square value.

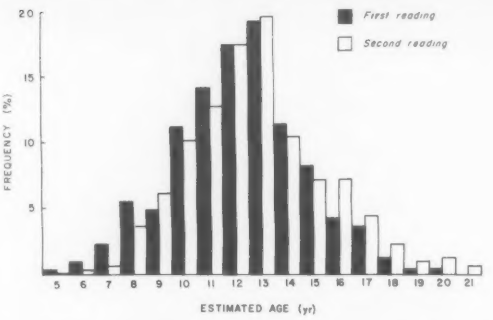

FIGURE 1.—Age composition of 322 yellowtail rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1973-74.

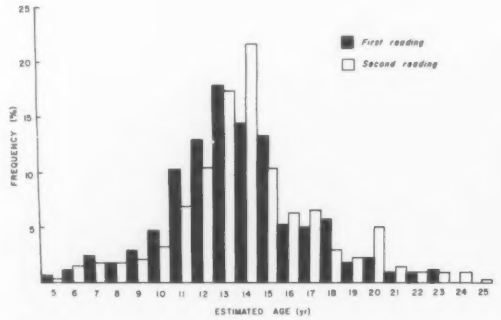

FIGURE 2.—Age composition of 353 canary rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1974.

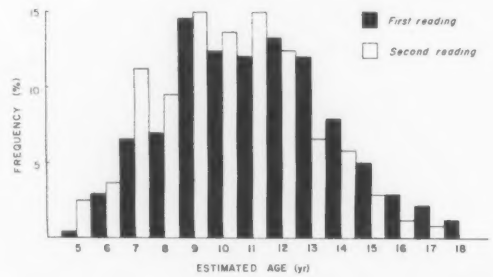

FIGURE 3.—Age composition of 242 black rockfish obtained by two independent readings of their otoliths; specimens were collected from fish processing plants in Astoria and Coos Bay, Oreg., 1974.

than ±1 zone. Kelly and Wolf (1959) reported 59.7% agreement ±1 yr for otoliths of 7–20+ yr-old redfish.

Several explanations exist for the observed deviations between readings. Due to the presence of split zones and the irregularity of the marginal areas on older rockfish otoliths, different readings may be obtained from different areas of the same otolith. There are eight major marginal areas on otoliths that can be used in age determination (Figure 4); two or three generally give superior results depending on the species in question. However, these favored areas are not consistently readable from one otolith to the next in any sample. Therefore, there is no specific area that can be used consistently on all the otoliths, making it possible that two different areas could be read on two independent readings of the same otolith. Indeed a comparison of areas used by readers A and B for yellowtail rockfish otoliths showed that of the readings that disagreed, 71% were made on different areas of the otolith, whereas, of the readings that agreed, only 56% were made on different areas.

Discrepancies in counts of annuli also are probably a function of the difficulty in defining the type of outer edge on otoliths. If an otolith had two opaque zones, each followed by a hyaline zone, plus an additional opaque zone on the outer edge, then an age of 2 was assigned. If an additional hyaline zone existed on the edge of the above otolith, then an age of 3 was assigned. But since the zones on the outer edge of older rockfish are indistinct because of slow growth at older ages, it is conceivable that discrepancies of 1 yr could exist between independent readings of the same area of a particular otolith.

A third cause of discrepant counts is that entire samples of otoliths were often exceptionally opaque, or, conversely, transparent, possibly due to the storage medium and/or length of storage. Annuli on otoliths such as these are difficult to distinguish.

Because one could question the use of only two readings to assess the consistency of otolith readings, a sample of 198 yellowtail rockfish otoliths was read independently three times with a week between readings. A chi-square test for independent data corrected for continuity indicated no significant differences among the three agreement statistics ($P>0.75$). In this case, consistency of readings was not changed by the addition of a third reading.

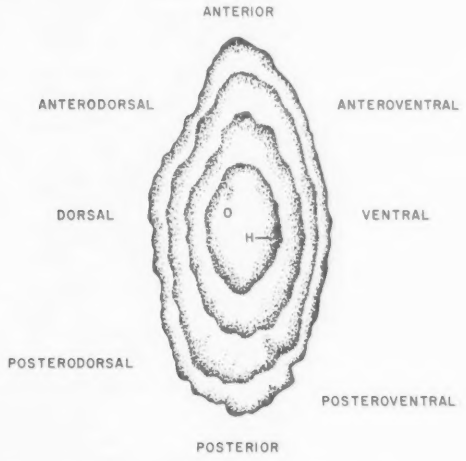

FIGURE 4.—Drawing of the right otolith (sagitta) from a 4-yr-old black rockfish as seen under reflected light on a dark background showing the marginal areas used in age determination (O-opaque zone; H-hyaline zone).

Validity of the Otolith Method

Until the data needed for validation can be collected, it is assumed for the purposes of this study that one opaque and one hyaline zone are laid down each year on otoliths of rockfishes in Oregon. Van Oosten (1929) and Graham (1956) listed methods used to provide indirect evidence of the validity of age readings of scales and other structures. The commonly applied methods are observation of a dominant year class over a period of years, and analysis of seasonal changes of the margin of some anatomical structure. Westrheim (1973) was able to follow the yearly progression of a dominant year class of *Sebastes alutus* for a period of several years and also demonstrated, by examination of the marginal zones on the otolith, that the hyaline zone is formed annually on juvenile fish. Kelly and Wolf (1959) found that one opaque and one hyaline zone are laid down each year on otoliths of young *S. marinus*.

Unfortunately, similar tests could not be conducted in this study owing to the absence of any obviously dominant year classes in the fish sampled and to the inadequate samples of young fish from a sufficient number of months throughout the year to permit demonstration of the seasonal changes in the margin of the otolith. Otoliths from older rockfish are not suitable for

this method, because zones on the outer edge are narrow and therefore difficult to distinguish until late in the growing season. Moreover, because of the irregular growth of otoliths of older rockfish, different marginal areas provide different results.

Otolith Sections

Results indicate that consistency of otolith readings is superior to that of scales or other structures for the three species of rockfishes studied, but agreement of otolith readings still may be unsatisfactory. Otoliths were sectioned to try to improve consistency of readings. Blacker (1974) noted that annuli are laid down only on the proximal (internal) surface of the otolith during later years in the life of fishes such as sole, *Solea solea;* plaice, *Pleuronectes platessa;* turbot, *Scophthalmus maximus;* redfish, *Sebastes* sp.; and horse mackerel, *Trachurus trachurus.* These annuli are not seen when the distal surface of the otolith is used for age determination and the investigator underestimates the age of the fish.

Exact agreement between readings of whole and sectioned otoliths of canary rockfish (37 vs. 21%) differed by 16 percentage points (Table 4). A chi-square test for paired data corrected for continuity revealed that there was a significant difference between the two ($P<0.025$). Percent agreement between first readings of whole and sectioned otoliths was low with a value of 51% ±1 assumed annulus. The similarity of the mean estimated ages indicates that the phenomenon reported by Blacker (1974) probably does not occur in canary rockfish otoliths. Ages were not substantially underestimated by reading the distal surface of the whole otolith.

Sectioning did not improve consistency of readings of canary rockfish otoliths. Moreover, it is not possible to follow specific annuli completely around the sectioned otolith to determine if an assumed annulus is split. Whole otoliths allow the reader a choice of marginal areas to read, whereas sections do not.

Additional treatments were applied to otoliths and scales with little success (Table 5).

TABLE 4.—Percent agreement between first and second readings of whole otoliths and between first and second readings of sectioned otoliths, and percent agreement between first readings of whole and sectioned otoliths of canary rockfish caught off Oregon, 1974.

	Within technique		Between techniques
Agreement	Whole	Sectioned	(Whole vs. sectioned)
Exact	37	21	21
±1	71	57	51
N	91	91	91
Mean estimated age	14.0	14.7	

TABLE 5.—Treatments applied to otoliths and scales of yellowtail, canary, and black rockfishes captured off Oregon during 1972-75.

Treatment	Description	Result
	Otoliths	
Baking	Lawler and McRae (1961)	Resolution not improved
Burning	Christensen (1964)	Difficult to obtain consistent effect
Scanning electron microscopy	Liew (1974), Blacker (1975)	Impracticable to view entire otolith in detail
Surface microscopy	Smith (1968)	Zones indistinct
Alizarin red S staining	In 1% KOH to obtain purple color	Stain not readily absorbed
Methyl violet stain	Albrechtsen (1968)	Stain absorbed, but zones indistinct
Silver nitrate stain	1% aqueous solution	Stain not absorbed
	Scales	
Polarized light microscopy	Kosswig (1971)	Zones near focus indistinct

Effect of Deviations of Otolith Readings on Biological Information

Age Composition

The frequencies of two independent readings of yellowtail rockfish otoliths made by different readers generally correspond for ages 9-15 (Figure 1). Correspondence is lower for younger and older age-groups. The two distributions are approximately normal with means of 12.2 and 12.8 yr, respectively. Figure 5 graphically demonstrates that the means are not significantly different because the 95% confidence intervals for the means overlap. For the two distributions, the standard deviations are similar and the ranges are equal, but the minimum and maximum values disagree by 1 yr (Figure 3).

Frequencies of age readings for canary rockfish derived from two independent readings by the same person correspond over most of the ranges of ages (Figure 2). Greatest discrepancies occurred at ages 11, 14, and 20. Again the distributions are approximately normal with means of 13.6 and 14.2 yr for first and second readings, respectively. The means are not significantly different at the 95% level (Figure 5). The standard deviations are similar, while the maximum ages disagree by 2 yr.

Otolith reading frequencies for two independent readings by the same person for black rockfish correspond closely for ages 9-12. There is less agreement for other ages (Figure 3). The

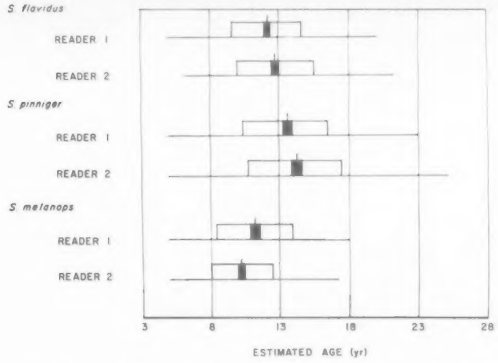

FIGURE 5.—Mean (vertical line), range (horizontal line), standard deviation of the mean (white bar), and 95% confidence intervals about the mean (black bar) for two otolith age readings of yellowtail rockfish, canary rockfish, and black rockfish landed in Oregon, 1973-74.

distributions are approximately normal with means of 11.1 and 10.2 yr, respectively, for first and second readings. Figure 3 shows the means to be significantly different at the 95% level. The standard deviations of the two distributions differ more for this species than for yellowtail and canary rockfishes. Ranges of the two distributions are similar (Figure 5).

Survival

Estimates of survival obtained by two methods generally correspond for all species and readings, although Chapman-Robson estimates were consistently lower than catch curve estimates (Table 6). At the 95% level none of the paired estimates from the two readings were significantly different, as shown by the overlap of confidence intervals. Differences between survival estimates calculated from readings of the same otoliths were greatest for yellowtail rockfish and smallest for canary rockfish by either the catch curve or the Chapman-Robson method; yet, on the average, differences between catch curve estimates for the two readings were greater than those obtained by the Chapman-Robson method (Table 6). The differences between catch curve estimates were 0.11, 0.015, and 0.093 for yellowtail, canary, and black rockfishes, respectively, while differences between Chapman-Robson estimates were 0.051, 0.031, and 0.051, respectively.

Age-Length Relationship

The age-length relationships derived from two otolith readings for yellowtail rockfish were described by the equation $L = cA^b$ (Figure 6). Fitted lengths-at-age for the first reading were slightly higher than those for the second reading, but 95% confidence limits of the estimates of constants c and b overlap considerably for the first and second readings (Table 7). Little or no overlap of confidence limits for constants c and b exists for males and females for either the first or second readings (Table 7), indicating a significant difference between the age-length relationships by sex for yellowtail rockfish. Age-length data for yellowtail rockfish were initially applied to the von Bertalanffy growth-in-length equation, but were not well described by this equation due to the lack of young fish in the samples.[6]

Age-length relationships for male canary rockfish based on two independent readings are nearly identical (Figure 7). Growth curves for females are similar (Figure 7), but discrepancies exist at older ages where fitted lengths for the first reading were higher than those for the second.

[6]The von Bertalanffy equations derived from two readings of yellowtail rockfish otoliths were:

Males—Reading 1: $l_t = 47.96[1 - \exp(-0.16(t + 4.01))]$

Reading 2: $l_t = 46.34[1 - \exp(-0.27(t - 1.03))]$

Females—Reading 1: $l_t = 55.47[1 - \exp(-0.14(t + 3.19))]$

Reading 2: $l_t = 53.81[1 - \exp(-0.19(t - 0.24))]$.

TABLE 6.—Survival estimates based on two independent readings of the otoliths of yellowtail rockfish, canary rockfish, and black rockfish landed in Oregon, 1973-74.

	Chapman-Robson			Catch curve				
Species	Estimate	SE	95% conf. limits	Estimate	SE	95% conf. limits	R^2	Ages used
Yellowtail rockfish:								
Reading 1	0.54	0.04	0.46-0.61	0.60	0.04	0.49-0.70	0.95	14-18
Reading 2	0.59	0.03	0.52-0.65	0.71	0.05	0.59-0.82	0.90	14-18
Canary rockfish:								
Reading 1	0.67	0.03	0.62-0.72	0.73	0.04	0.65-0.80	0.86	15-23
Reading 2	0.70	0.02	0.65-0.75	0.74	0.04	0.66-0.82	0.85	15-23
Black rockfish:								
Reading 1	0.60	0.03	0.54-0.66	0.67	0.02	0.62-0.72	0.98	12-17
Reading 2	0.55	0.04	0.47-0.63	0.58	0.03	0.52-0.64	0.97	12-17

TABLE 7.—Estimates of parameters describing the age-length relationship for yellowtail rockfish, canary rockfish, and black rockfish based on two independent readings of their otoliths. The 95% confidence limits for the estimates are in parentheses.

Parameters	First reading	Second reading
♂ yellowtail rockfish:		
c	28.00	28.41
	(25.96-30.03)	(26.37-30.45)
b	0.18	0.17
	(0.15-0.21)	(0.14-0.20)
♀ yellowtail rockfish:		
c	25.08	23.66
	(23.05-27.12)	(21.62-25.71)
b	0.26	0.29
	(0.23-0.30)	(0.25-0.32)
♂ canary rockfish:		
L_∞	53.60	53.30
	(52.38-54.82)	(52.14-54.46)
k	0.19	0.18
	(0.17-0.21)	(0.16-0.20)
t_0	0.68	0.54
	(0.39-0.97)	(0.25-0.83)
♀ canary rockfish:		
L_∞	60.95	57.43
	(58.09-63.81)	(55.90-58.96)
k	0.15	0.18
	(0.12-0.17)	(0.15-0.20)
t_0	0.54	0.90
	(−0.03-1.11)	(0.49-1.30)
♂ black rockfish:		
L_∞	50.30	52.03
	(49.07-51.53)	(50.48-53.58)
k	0.23	0.22
	(0.21-0.26)	(0.19-0.25)
t_0	−0.46	−0.44
	(−0.65)-(−0.28)	(−0.62)-(−0.26)
♀ black rockfish:		
L_∞	57.83	58.78
	(55.30-60.36)	(56.43-61.13)
k	0.17	0.18
	(0.14-0.19)	(0.15-0.20)
t_0	−0.74	−0.56
	(−0.99)-(−0.49)	(−0.77)-(−0.35)

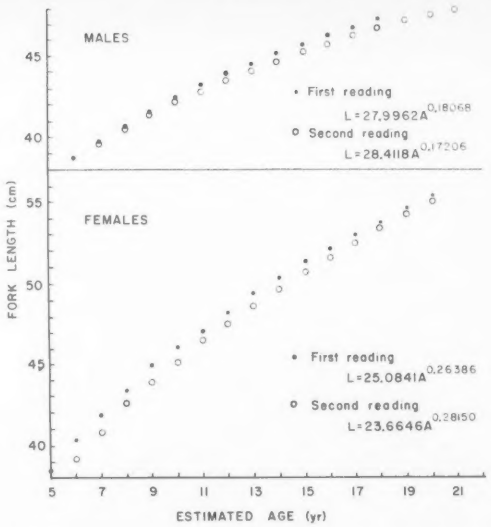

FIGURE 6—Age-length relationships for yellowtail rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1973-74.

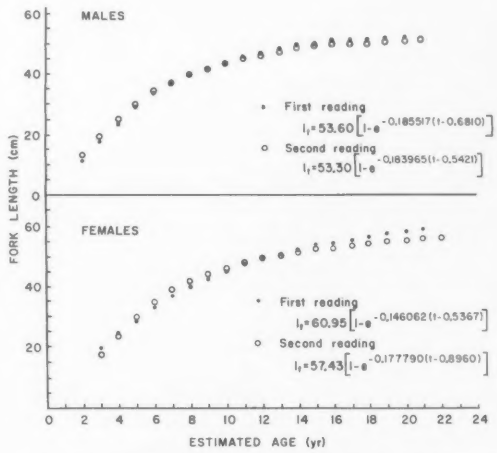

FIGURE 7.—Age-length relationships for canary rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1972 and 1974.

This difference exists because the first reading was generally lower than the second, and readability decreased with age. Interval estimates of the von Bertalanffy constants L_∞, k, and t_0 for first and second readings for males are comparable (Table 7). Greater differences occur between estimates of the parameters for first and second readings for females, although interval estimates still overlap. For males and females for the first reading, there is no overlap of interval estimates for L_∞, slight overlap for k, and considerable overlap for t_0 (Table 7). Similarly, for males and females for the second reading, there is no overlap of interval estimates for L_∞, and considerable overlap of interval estimates for k and t_0. This indicates that differences in growth exist.

Growth curves for male black rockfish derived from two otolith readings are similar (Figure 8), although discrepancies existed between fitted lengths at older ages. The same is true for the age-length relationship for females (Figure 8). Interval estimates of all three von Bertalanffy constants overlap considerably (Table 7), indicating no significant differences between growth curves obtained from the two readings. For males and females for the first reading, there is no overlap of interval estimates for L_∞ and k, and considerable overlap for t_0. For males and females for the second reading, there is no overlap of interval

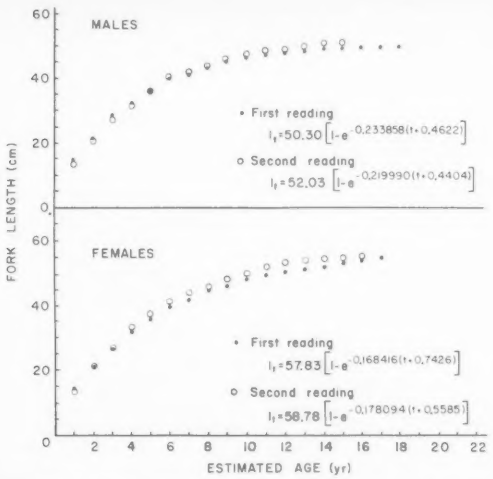

FIGURE 8.—Age-length relationships for black rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1973-75.

estimates for L_∞, slight overlap for k, and considerable overlap for t_0. As was found for yellowtail and canary rockfishes, sexual differences in growth of black rockfish are apparent.

Further support of the otolith method may be evidenced by a comparison of mean lengths-at-age obtained in this study with those of other investigators. Phillips (1964) and Westrheim and Harling (1975) reported mean lengths similar to those obtained in this study for yellowtail rockfish (Table 8). A similar correspondence of canary rockfish lengths does not exist, where an increase of values from north to south is noted. This analysis is limited by small sample sizes and could further be complicated by geographical differences in growth reported to exist for other species of rockfishes in the Northeast Pacific (Westrheim and Harling 1975).

In summary, the observed deviations between otolith readings produced slightly different estimates of survival and of age-length relationships, although these differences were not statistically significant. The otolith method is the most reliable of those analyzed and we believe, with some reservations, that it can be used reliably for management purposes. The reader should be cautioned that contrary to the results of the statistical test, some of the survival estimates appear to be substantially different (Table 6). Possibly a Type II error exists (Snedecor and Cochran 1967), i.e., the statistical test shows no significant difference when, in fact, one exists. We believe that, for the most part, the observed deviations between readings are minor; moreover, with the collaboration of two or more trained readers, consistency of age determinations can be improved.

Further studies establishing the validity of the technique are warranted. This may be made possible by analysis of the marginal growth of the otoliths of juvenile rockfish. By providing evidence that an opaque and an adjacent hyaline zone truly constitute an annulus, accuracy of otolith age determinations will be ensured.

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TABLE 8.—Mean length (centimeters) at selected ages of yellowtail rockfish and canary rockfish from British Columbia, Oregon, and California. Numbers of fish are shown in parentheses.

		British Columbia (Westrheim and Harling 1975)		Oregon (This study—reading 1)		California (Phillips 1964)
Species	Age	Male	Female	Male	Female	Sexes combined
Yellowtail rockfish	5	27.1 (16)	27.6 (10)	—	30.0 (1)	31.9 (116)
	10	42.3 (4)	41.0 (2)	42.9 (15)	46.6 (19)	43.0 (48)
	15	46.6 (18)	49.2 (7)	46.1 (17)	50.4 (8)	50.4 (6)
	20	47.6 (8)	—	—	53.0 (1)	—
Canary rockfish	5	22.5 (1)	23.5 (1)	29.0 (8)	29.2 (26)	31.9 (128)
	10	—	38.5 (1)	44.7 (11)	48.0 (6)	46.8 (57)
	15	—	—	49.2 (32)	52.4 (12)	56.5 (7)
	20	50.5 (1)	—	51.0 (2)	56.0 (6)	—

Abramson supplied the von Bertalanffy computer program, BGC-2; and J. K. Andreasen provided the graphical program FISHPLOT.

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PREDATOR-PREY INTERACTIONS IN SCHOOLING FISHES DURING PERIODS OF TWILIGHT: A STUDY OF THE SILVERSIDE *PRANESUS INSULARUM* IN HAWAII[1]

PETER F. MAJOR[2]

ABSTRACT

Observations of free living and captive silversides were made in Kaneohe Bay, Hawaii, in October and November 1972 and September 1973. The silversides demonstrated changes in schooling behavior associated with changes in light levels during the periods of twilight. During morning twilight, individual silversides formed schools, which in some areas moved from deep water to shallow water over reefs. All silversides remained in large inactive schools in shallow water or along the edge of channels throughout the day. During evening twilight, schools left the reef and/or broke up, with individual silversides spreading out to feed near the surface. Predation upon the silversides, as evidenced by their jumping behavior, was most intense during the twilight periods as schools formed and broke up. Captive silversides, when not in the presence of predators, tended to increase their interfish distance when in diurnal schools. The formation and breakup of schools of these silversides appear to be very similar to behavioral patterns of related and unrelated species of fish in many parts of the world. The formation and break up of silverside schools appear to be related to the threat of predation, the availability of the silverside's food, and the visual sensitivity and thresholds of both the silversides and their predators.

Daily twilight or crepuscular periods are critical ones with respect to predator-prey interactions between many species of fishes, at least in tropical regions of the world. Hobson (1968, 1972), Collette and Talbot (1972), and Domm and Domm (1973) demonstrated the importance of twilight periods on behavioral changes in reef fishes. Hobson (1968, 1972, 1974) suggested that such transitions in behavior are shaped by the threat of predation.

Predation pressure is also clearly a factor in the evolution of schooling behavior in prey species (Breder 1959, 1967; Hobson 1968; Shaw 1970; Radakov 1973). Most reef fishes hide from their predators amongst the interstices of the coral reef. Many surface and open water prey species lack such hiding places and appear to form schools as a means of cover seeking (Williams 1964, 1966), the school serving as a mobile biological refugium especially during daylight hours. During evening twilight periods many such schools break up with individuals spreading out to feed. During morning twilight periods individuals once again form schools (Hobson 1968, 1972, 1973; Hobson and Chess 1973).

Vision has been shown to be important in the maintenance of schools (Woodhead 1966; Hunter 1968; Shaw 1970; Radakov 1973). In addition, Munz and McFarland (1973) indicated that the behavioral changes of tropical marine fishes during periods of twilight are due to shifts in the visual sensitivity of these fishes with changes in light levels.

The objectives of this study were to determine if schools of the Hawaiian silverside, the iao, *Pranesus insularum*, broke up and reformed in response to light levels occuring during twilight, and to determine how the activity of predators of this species of silverside was related to this behavior.

Study Sites

Field observations were made at two locations within Kaneohe Bay, along the island of Oahu in the Hawaiian chain. These sites were a 10,000 m^2 area of flat reef (water depth ≤2 m at high tide) immediately adjacent to the east side of Lilipuna Pier (Dock), and a 2,500 m^2 area near the central portion of a dredged out (to a depth of 2-3 m)

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[2]Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064; present address: Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6.

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"lagoon" adjacent to the Hawaii Institute of Marine Biology (HIMB) on Coconut Island. The northern edge of the reef adjacent to Lilipuna Pier drops abruptly into a 3- to 10-m deep channel, while the southern side is adjacent to the shore.

The reef and channel area near Lilipuna Pier are open to the effects of wind and waves within Kaneohe Bay throughout the year. Occasionally, the winds abate or shift and the bay's surface becomes calm and glassy. The observations reported here could only be made at such times when the estimated wind velocity was less than 2.6 m/s (5 knots). At night near the end of the pier a fixed low intensity incandescent light bulb casts an arc of light out over a small area in the channel. Observations were not made within the area encompassing this arc of light. The waters in the HIMB lagoon are usually calm or only slightly rippled, being protected by a vegetation covered coral rubble peninsula on its normally windward side and thicker, higher, vegetation on its island or leeward side.

Kaneohe Bay is rimmed at approximately 1.6 km inland by mountains that rise to 762-960 m. Throughout each day, dense clouds usually form along these mountains, occluding the sun during the late afternoon. This often results in twilight conditions occurring earlier than would normally be predicted for the bay's position of latitude and longitude.

METHODS

The prey species of fish observed in this study was *P. insularum*, approximately 20-60 mm SL and approximately 0.03-2.45 g wet weight. Observations of the silverside's behavior were made during calm periods in October (7 days) and November (3 days) 1972 and September (5 days) 1973. All observations were made visually from a height of 0-3 m above the surface of the water. The morning observations commenced approximately 115 min prior to the time of sunrise. The evening observation period terminated about 60 min after the time of sunset.

The only attribute monitored quantitatively during the course of the observations was the jumping escape behavior of the silversides in response to attacking predatory fishes. Enumerating the jumps became a shorthand method of quantifying the number of predatory attacks in the calm areas studied because jumping was observed to be the primary means of escaping predators once an attack occurred. *Pranesus insularum* was the only prey species observed to jump in the above areas during the periods of this study. The success of predators at capturing prey during the attacks was not determined. Hobson (1968) used a similar method to quantify the number of times leaping predatory cabrilla, *Mycteroperca rosacea*, attacked flatiron herring, *Harengula thrissina*, in the Gulf of California.

During periods of darkness or reduced light, when visual observations under existing light were not possible, jumping by schools of prey could be heard within the areas studied by careful listening; this could only be done when there was no wind and the surface of the water was calm. The time at which schools broke up or reformed during twilight was estimated by listening to changes in the sound of jumps made by multiple and single prey close by, or with a flashlight beam which was quickly turned on and off in one spot, or swept rapidly across the surface of the water from above, and/or held underwater within 0.3 m of the surface. Whether the silversides were schooling or spread out could be readily determined when the fish were illuminated by the beam of light.

Light measurements were made above the surface of the water with a photometer (Weston Ranger 9 universal exposure meter).[3] Readings taken with this photometer were compared with those made with a Gossen foot-candle meter and a Spectra-Combi 5000 Model photometer (Photo Research, Burbank, Calif.). The readings obtained during twilight periods were comparable to those given by Brown (1952).

The observations and events reported here are related to the time of sunrise, sunset, and the periods of morning and evening civil and nautical twilight. The two periods of twilight are defined by the angular distance of the sun below the horizon, 0° to −6° for civil twilight, and −6° to −12° for nautical twilight. Fish respond directly to the amount and type of light present, which is influenced by astronomical as well as local environmental conditions. However, the use of these terms and that of the corresponding angular distance of the sun below the horizon is of immense value when comparing the observations of many investigators working in different loca-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tions at different times of the year and under different environmental conditions.

BEHAVIOR OF FREE-LIVING SILVERSIDES

Between sunrise and sunset each day hundreds to thousands of individual silversides could be observed in large, often elongated, schools along Lilipuna Pier and other structures over shallow reefs, along the edge of reefs, and in quiet protected waters such as the HIMB Lagoon. At times the silversides remained in the shadow of structures or overhanging vegetation, rarely venturing into sunlit water. The schools were located just under the surface of the water, with individuals often forming single or multitiered layers. The schools as a whole were largely stationary and inactive except for the occasional individual that darted out from and immediately returned to a school. These individuals appeared to be feeding, snapping at objects which I could not see when they left the school. While in the large inactive schools, individuals about one-half to two body lengths apart were randomly oriented to one another. However, upon the approach of a predator or potential predator, or when attacked, the individuals rapidly became polarized, often less than a body length apart as the school maneuvered about the predator(s) in well coordinated patterns.

When a predator slowly approached a school of silversides it frequently penetrated into the school. However, as the predator moved into and through a school, the silversides split into two or more smaller groups which passed around to the sides of the predator to reunite behind and along the path just traversed by the predator. This maneuver resulted in the formation of a void or halo of clear water around the entire predator as it moved through the school. This halo was estimated to average about one to two predator body lengths in width in any direction from the predator. Similar behavior has been reported and illustrated by Breder (1959), Nursall (1973), and Radakov (1973). When a predator actually attacked, it usually dashed at high speed toward an individual in or near a school or into a segment of a school. When attacked, individuals in the immediate area of the predator jumped out of the water as they radiated out and away from the path of the predator. In a larger school, silversides at increasingly greater distances from the attacking predator jumped less, the jump(s) grading into evasive swimming; and in some instances, little or no initial response was made by individuals some distance from the predator.

As jumping silversides reentered the water they realigned with other silversides that had jumped or evaded by swimming. At the same time there was a general, though somewhat belated, movement of individuals around into the wake of the rapidly moving predator. When an attack was prolonged, as when a predator chased an individual or small group of silversides, a large school often formed a number of smaller schools, which occasionally coalesced later. Frequently, jumping and/or evading individuals or segments of the attacked school joined with one or more other schools which were usually nearby but unaffected by the predator(s).

When a predator, such as a barracuda, attacked from a horizontal direction, the silversides usually had a strong lateral component to their jumps. Such jumps usually occurred at a shallow angle just above the surface and less than 45° to the surface. When attacked from directly below, initial jumps tended to have a somewhat more vertical than horizontal component, being greater than 45° to the water's surface. Distances covered during single horizontal jumps were not measured, but may have been as great as 5-10 times an individual's body length; several meters were spanned during a series of jumps.

When more than one predator simultaneously approached or attacked a school of silversides, evasive maneuvering and jumping became confused. The more rapidly increased numbers of predators approached or attacked, the more "disorganized" the silverside's evasive response appeared to become.

In Kaneohe Bay the most common diurnal predators observed attacking and chasing silversides were barracuda, *Sphyraena barracuda*; blue jack, *Caranx melampygus*; leatherjacket, *Scomberoides lysan*; and lizardfish, *Saurida gracilis*. Needlefish, *Tylosurus* sp., were also observed near silverside schools, but attacks were not seen. During the day, and particularly during the evening twilight period, the jack, *Caranx ignobilis*, may also have been a predator. This jack readily attacked silversides in field and cement enclosures. Recently ingested silversides were occasionally found in the stomach contents of

young scalloped hammerhead shark, *Sphyrna lewini* (45-90 cm TL), caught by gill net at night in the channels of Kaneohe Bay.

Solitary barracuda and needlefish slowly cruised along just under the surface of the water when they were near schools of silversides. When stalking, they usually remained relatively motionless as they drifted or used slow caudal fin undulations to scull along the surface. The barracuda attacked by quickly dashing, usually horizontally, a short distance towards an individual or school of silversides.

Individuals or schools of jacks and leatherjackets usually swam near the bottom in the lagoon or at some midwater depth in the deeper channels near Lilipuna Pier. Individuals of these species slowly approached or rapidly attacked the silversides, usually at an angle of about 45° to the surface. They immediately retreated towards the bottom after their approach or attack.

Lizardfish are cryptically colored, solitary benthic "sit and wait" predators. When a school of silversides swam over a lizardfish, it usually dashed at an angle nearly perpendicular to the surface, or at an angle greater than about 45° to the surface as it approached the silversides.

Because the silversides were located just under the surface of the water, the attacks by their predators could usually be detected in one or both of two ways. The momentum of a rapidly moving predator often carried it clear out of the water during an attack. This was particularly evident during attacks made in a vertical direction. If the predator turned as it approached the surface, its body and/or caudal fin usually created a boil of water at the surface, which often erupted with a popping sound into a splash or spray of water. If it was calm, a boil of water often left a small area of residual foam bubbles as concentric circles moved out across the water. When chases occurred along or near the surface, the predators often left a wake of disturbed water and froth to mark its path of pursuit.

In the Lilipuna Pier area an infrequent diurnal aerial predator was also observed. One to four common noddies, *Anous stolidus pileatus*, remained near or on the pier and flew to the areas of jumping silversides and attempted to catch them while the fish were still at the surface. Noddies were more successful at catching silversides when predatory fish attacked and then chased the silversides along the surface.

BEHAVIOR OF CAPTIVE SILVERSIDES

Over 100 h of observations of captive silversides in net enclosures (3 m × 3 m × 3 m deep to 6.1 m × 6.1 m × 2 m deep) in the lagoon in Kaneohe Bay and in a circular cement tank (9 m in diameter and 3 m deep with an underwater viewing window) were made during day and night periods. Within several days after introduction into the enclosures that lacked predators, the individuals in the schools of silversides slowly increased their interfish distances from less than one or two body lengths (as seen in the field) up to distances of 5-10 body lengths or more. Although the individuals were often randomly aligned with respect to each other, they did not lose their polarity to one another when a school moved. Individuals occasionally fed during the day, much as they did when free in the field. However, they did not dash out towards an object and immediately return to a school. When one or more predators, such as jacks or barracuda, were introduced into an enclosure the schools tightened as interfish distances between silversides decreased to less than one to two body lengths. Individuals continued to dart out from the relatively stationary and motionless schools, much as they did in the field. If attacks or approaches were not initiated by a predator, the schools loosened as interfish distances increased once again. These distances were not as great as they had been prior to the introduction of the predator(s). Feeding continued until approaches or attacks occurred. When approached, schools split and formed a halo around the predator as they moved to the rear of the predator to reform a school again. When attacked, individuals jumped out of the water and across the surface, away from the predator. The behavior of individuals and schools of silversides in the enclosures was much the same as that observed in the field, as described above.

During evening twilight periods, interfish distances increased as individuals in the schools spread out across the surface. During the twilight period, I could see the prey silhouetted against the evening sky, but not the predators against the bottom. As darkness increased, it rapidly became impossible to see the silversides as well, although the boils of water and splashes made by an attacking predator and the return of jumping prey into the water could be heard. During morning

twilight, interfish distances decreased as polarized schools once again formed and moved in coordinated patterns as they did in the field.

Silverside Jumping Activity Patterns

Morning Twilight

In the Lilipuna Pier area prior to nautical twilight, I could hear jumping silversides and the "pop" associated with attacking predators striking the water's surface approximately 20 min after the observation periods had commenced and 95 min prior to sunrise (Figure 1). These jumps were made primarily by individual fish in close proximity to the pier in the channel near the edge of the reef. Jumping occurred later by increasingly larger numbers of individuals in schools at the easternmost end of the observation area. Jumps occurred initially near the edge of the reef, moved toward, then turned northwest parallel to and along the shore, finally spreading out over the reef and toward the pier. These attacks by predators and jumps of silversides sequentially traced three sides of the perimeter of a rectangle defining the east, south, and west boundaries of the observed area near the pier. Attacks and jumps in shallow water over the reef predominated after the beginning of nautical twilight, and by sunrise all attacks and jumping occurred within a few meters of the pier. Peak activity in shallow reef and deep channel water was recorded just after the beginning of civil twilight and steadily decreased to midday levels (Figure 1).

The only predators observed to attack the silversides over the reef in the early morning were lizardfish. Blue jacks and barracuda were observed in the channel and occasionally over the reef near sunrise and during the late morning.

In the lagoon area, jumps in the central deeper area of the lagoon were initially recorded 45 to 50 min before sunrise (Figure 1). As twilight progressed, jumping was eventually seen in narrow bands of shallow water along the sides of the lagoon, but occurred infrequently. Barracuda and jacks were the principal early morning predators, although lizardfish were also observed attacking the silversides. Since the shallows were relatively small in area, most of the silversides were concentrated over the central deeper water of the lagoon. A period of increased jumping activity did not occur in the lagoon during twilight as it did near the pier.

Light meter readings of 0.096-0.402 foot candle (Table 1) were made in 1973 during the time (18-24 min before sunrise, i.e., the time of civil twilight) when silversides were in the process of forming schools, especially in the lagoon area. Initial schooling became noticeable (individuals moving closer together, becoming more cohesive and polarized when swimming as they did during the day) in 1972 and 1973 as early as 44-23 min before sunrise and was completed as late as 33-18 min before sunrise (Table 2). Silversides then remained in schools throughout the day.

In summary, during the morning, predator attacks and silverside jumping could not be detected until 95 min before sunrise at the pier and 50 min before sunrise in the lagoon. Deepwater attacks were initially noted for individual silversides, but subsequently increased numbers of jumps were recorded in shallower water for increasingly larger schools, especially near the pier. During the time peak jumping occurred (30-10 min before sunrise), silversides were forming cohesive polarized schools (44-18 min before sunrise, mean 29.4 min).

TABLE 1.—Light levels (light meter readings in foot candle) and the breakup and formation of schools of silversides.

Type of activity	Author	Location	Species	Light levels		No. of readings	Remarks
				Mean	Range		
Breakup of schools	Steven 1959	West Indies	*Hepsitia stipes*	0.06	0.07-0.05	2	Fish in aquariums indoor with windows and door closed, no artificial light. Watched until nightfall.
	Shaw 1961	Marine Biological Laboratory, Mass.	*Menidia*	0.12	0.35-0.03	14	Experimental; gradual reduction of light until school began dispersing. Used neutral density filters.
	This report Sept. 1973	Kaneohe Bay, Hawaii	*Pranesus insularum*	0.21	0.402-0.035	3	Field, during evening twilight.
Formation of schools	This report Sept. 1973	Kaneohe Bay, Hawaii	*Pranesus insularum*	0.18	0.402-0.096	4	Field, during morning twilight.

[1]One-way analysis of variance (ANOVA) of all light meter readings ($P = 0.57$).

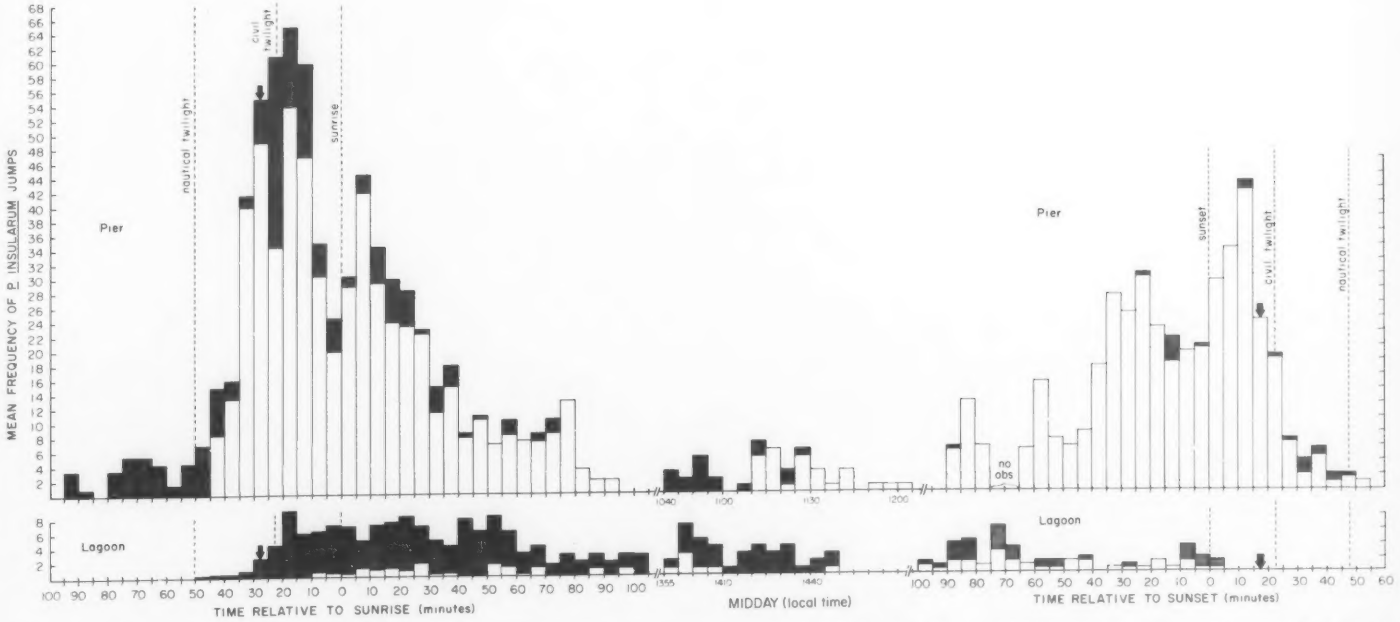

FIGURE 1.—Mean frequency of jumps (predator attacks) recorded for *Pranesus insularum* at 5-min intervals for Lilipuna Pier and HIMB lagoon areas. Times are presented relative to sunrise or sunset. Midday frequencies are presented with respect to local (real) time. The mean times of school formation in the morning and school breakup in the evening are denoted by the inverted arrows. Shaded bars denote deepwater (channel) jumps. Light bars denote shallowwater (reef) jumps. Double oblique slashes denote the breaks between morning, midday, and evening observations.

TABLE 2.—Comparison of school formation and breakup in *Pranesus insularum* with twilight phenomena recorded near Lilipuna Pier and HIMB lagoon, Kaneohe Bay, Hawaii.[1]

[Mean school formation = −29.4 min (before sunrise), mean school breakup = +19.1 min (after sunrise).]

Location	Date	Local time of sunrise (h)	Relative time of sunrise	Difference in time (minutes) between sunrise and: Beginning nautical twilight	Beginning civil twilight	Initial school formation	Schools formed
Lilipuna Pier	7 Oct. 1972	0625	0	−48	−23	−44	−33
HIMB lagoon	8 Oct. 1972	0624	0	−47	−22	−34	−24
	23 Oct. 1972	0629	0	−48	−22	−26	−20
	19 Nov. 1972	0644	0	−51	−24	−38	−31
	21 Nov. 1972	0646	0	−51	−24	−33	−28
	22 Nov. 1972	0647	0	−51	−24	−40	−33
	12 Sept. 1973	0617	0	−48	−21	−24	−18
	14 Sept. 1973	0619	0	−48	−21	−23	−21

Location	Date	Local time of sunset (h)	Relative time of sunset	Difference in time (minutes) between sunset and: End of nautical twilight	End of civil twilight	Initial school breakup	Complete school breakup
HIMB lagoon	8 Oct. 1972	1814	0	+48	+22	—	+26
	22 Oct. 1972	1804	0	+48	+22	+16	—
	13 Sept. 1973	1835	0	+48	+22	—	+24
	17 Sept. 1973	1832	0	+48	+22	+15	+21
	18 Sept. 1973	1932	0	+48	+21	+14	+18

[1]One-way ANOVA comparison of times of starting to school/schooling and starting to break up/complete breakup ($P = 0.004$).

Midday (1000-1500 H, Local Time)

In the pier area accurate counts of jumps made by the silversides during the time between 1000 and 1500 h local time were usually difficult to make due to waves caused by wind and nearby vessel activity.

Figure 1 presents the data collected during representative midday periods near the pier when interference was minimal. Generally, the silversides formed large elongated schools (hundreds to thousands of individuals) under or near the pier. The schools were largely inactive except when predators or potential predators such as barracuda, lizardfish, jacks, and needlefish, approached or attacked. When the tide level was low, the schools condensed and moved into deeper water near or under the end of the pier.

In the lagoon area at HIMB, the behavior and distribution of silversides was much the same during midday as it was near the pier (Figure 1). Small schools of silversides were strung out along the sides of the channel. Large schools of hundreds to thousands of fish were relatively inactive and concentrated over deeper water in the center of the lagoon. Barracuda and jacks were the most frequent predators, but lizardfish and leatherjackets were occasionally active in the lagoon.

Evening Twilight

As sunset approached, predator-prey activity increased in frequency in the pier area (Figure 1). Peak activity occurred between sunset and the end of the period of civil twilight and then declined rapidly to stop just after the end of the nautical twilight period. The silversides moved off the reef along, but in the direction opposite to, the path taken during the morning twilight movement onto and across the reef. Attacks and jumping occurred near the pier, then out over the reef, moved eastward along and parallel to shore, finally northward to the edge of the reef at the easternmost end of the observation area. As darkness increased, attacks and jumping gradually diminished in frequency and intensity (fewer individuals in smaller and fewer schools jumped).

In the lagoon area midday jumping activity in shallow and deep water continued until just after sunset, then stopped abruptly (Figure 1). The low number of jumps in deep water in the late afternoon and evening in the lagoon contrasts sharply with the frequency of jumps in the early morning (Figure 1). This difference may be related to the low levels of incident light striking the surface of the lagoon in the afternoon and evening due to the vegetation and the mountains and clouds to the northwest obscuring the sun. In the morning the lack of high vegetation and mountains nearby to the northeast resulted in light striking the lagoon's surface so that the silverside were presumably visible to their predators.

Light meter readings of 0.035-0.402 foot candle (Table 1) were made during the time (20-24 min

after sunset, i.e., during civil twilight) silverside schools were breaking up, the individuals spreading out just under the surface of the water. In 1972 and 1973 schools began to break up (increased interfish distances became noticeable) between 14 and 16 min after sunset and were spread out by 18-26 min after sunset (Table 2).

In summary, with the approach of dusk, predator attacks and silverside jumping increased in frequency and intensity to peak during the period of civil twilight, shortly after sunset, near the pier. In the lagoon there was no peak activity; the last attacks and jumps were recorded immediately after sunset. Peak jumping near the pier was recorded 5-15 min after sunset, just before the time the silverside schools were observed to break up becoming less polarized and cohesive (14-26 min after sunset, mean 19.1). In the lagoon, however, attacks stopped before the prey schools spread out; this may have been due to the shadows and increased darkness caused by heavy vegetation along the northwest side of the lagoon.

Silverside Behavior: Conclusions

The temporal pattern of predatory attacks and silverside jumping relative to sunrise was the mirror image of that relative to sunset, at least for the Lilipuna Pier area (Figures 1, 2). For each of the four environmental situations studied, Figure 2 simplifies and graphically presents (at 50-min intervals) the mean frequency of silverside jumps illustrated in Figure 1. Midday (1000-1500 h) jumps were combined and were not divided into 50-min intervals. Statistical comparisons (analysis of variance, $P \leq 0.05$) of the jumping data for sunrise (−50 to +50 min), midday, and sunset (−50 to +50 min) for each of the four situations indicated that, at least for the shallow-water reef area near Lilipuna Pier, the frequencies of jumps at sunrise and sunset were similar and differed from the number during midday.

The mean time of school formation occurred just prior to the beginning of civil twilight in the morning, and the mean time of the breakup of schools occurred just before the end of civil twilight in the evening. Peak predator activity occurred just after schools formed (mean time) in the morning and just prior to their breakup (mean time) in the evening. The data presented indicate that related events (e.g., school formation versus breakup) occurred in the study sites significantly

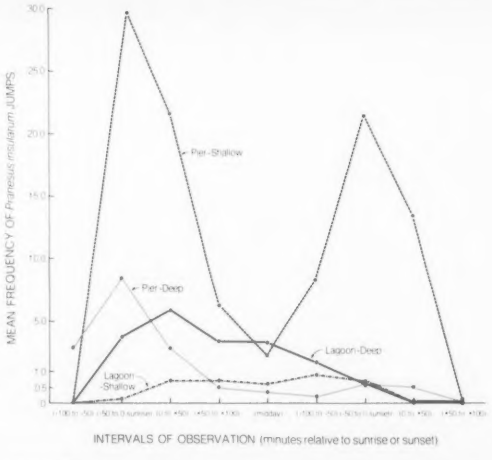

FIGURE 2.—Mean frequency of *Pranesus insularum* jumps for nine 50-min intervals (except midday). Based on data also presented in Figure 1.

earlier (about 5-15 min) in the evening, relative to sunset compared with the morning events, relative to sunrise (Table 2). This discrepancy may be due to the shadow effect of the clouds and mountains near Kaneohe Bay, which produce evening twilight conditions 5-15 min earlier than predicted, as discussed above. The relatively low frequency of deepwater attacks near the pier in the evening indicated that by the time silversides had moved off the reef and/or spread out, it may have been too dark for predators to see individual silversides. In the morning, the lack of mountains and vegetation and increasing light levels resulted in sufficient light being available for predators to see their prey.

Observations of free-living and particularly captive silversides, as well as my observations of other schooling prey species (striped mullet, *Mugil cephalus*, and Hawaiian anchovy, *Stolephorus purpureus*) in Hawaii, indicate that predation is of prime importance in shaping the behavioral patterns of prey species. When held captive in the absence of predators for days or weeks, individual prey in schools increased their interfish distances and appeared to feed more actively than they did in the field. When predators were present, interfish distances within captive schools were similar to interfish distances between individuals in the field. During the day, schooling behavior appears to serve a protective function for individuals, reducing the number of

attacks made by predatory fish. This protective function has also been observed for other schooling prey species (Radakov 1958, 1973; Neill and Cullen 1974). The chance that a predator has of singling out a specific individual silverside are greatly reduced if schools are formed. This appears to be especially true when the prey are polarized towards one another and move close together through coordinated maneuvers. In the field, when predators were not in the immediate vicinity of silverside schools, individual silversides became relatively motionless and randomly oriented towards one another, darting out from schools presumably to feed. When individual silversides presumably became exposed and/or appeared to be accessible to one or more nearby predators, the predators approached or attacked. If the predator's approach was slow, the individual silversides became polarized, the school maneuvering evasively. If a predator's approach was sudden or rapid, individual silversides jumped out of the water one or more times to evade. Both schooling and jumping presumably decrease the time a predator had to align itself with a specific individual prey. In addition, a jumping silverside often landed in the midst of its own, or that of another nearby, school, presumably disappearing from the predator's field of vision and/or path of swimming. The formation of large schools composed of many hundreds or thousands of individuals, especially a number of such schools relatively close to one another, appeared to increase an individual silverside's chance of escape when jumping.

The movement of silversides into the shallow water over reefs, and their location near and under Lilipuna Pier and heavy overhanging vegetation and along the sides of the lagoon, may be additional means, besides schooling, of reducing predation. In the shallow water near the pier, the most common vertical attacking predators were lizardfish. In deeper water in the lagoon and near the pier, jacks and leatherjackets also attacked vertically. Horizontal stalking and attacking predators, such as barracuda and needlefish, occurred in both deep and shallow water. The depth of water over the reefs may have been less than sufficient for some of the vertical attacking species to maneuver and approach schools of silversides undetected. The occurrence of silversides near structures and along the sides of the lagoon may have also limited the maneuverability and avenues of approach for all species of predators.

DISCUSSION

The interactions between silversides and their predators in relation to solar phenomena are almost identical in pattern and time to those given by Hobson (1968, 1972) for the interactions of *Harengula thrissina* and their predator *Mycteroperca rosacea* in the Gulf of California. Hobson and Chess's (1973) study of the arrival and departure of *Pranesus pinguis* to and from reefs at Majuro Atoll in the Marshall Islands also showed school movement related to specific times during twilight. However, only a few predatory attacks were observed at Majuro Atoll. Comparisons of lunar and tidal changes during the studies in Kaneohe Bay and Majuro Atoll and Baja California seem to indicate a relatively minor influence on the crepuscular behavior of schools.

Hobson (1968, 1972, 1973), Collette and Talbot (1972), and Domm and Domm (1973) have demonstrated that there is relatively little activity amongst most coral reef fishes during a specific segment of the twilight period. In the morning, nocturnally active reef fish leave the open water column to hide in the coral reef approximately 30 min before sunrise (Hobson 1972). Diurnal species do not reoccupy the water column until approximately 12-16 min prior to sunrise. It is exactly between the above times, the "quiet period," as defined by Hobson (1972), that peak surface predator-prey activity and school formation takes place in Kaneohe Bay, just as it does in the Gulf of California (Hobson 1968, 1972), and possibly Majuro Atoll (Hobson and Chess 1973). The pattern is reversed during evening twilight (Hobson 1972). Diurnal reef species evacuate the water column approximately 6-22 min after sunset. Nocturnal species then reoccupy the water column about 14-34 min after sunset. Again, surface predator-prey interactions peak and schools break up in Kaneohe Bay during the time that would be comparable with the evening quiet period in other parts of the world.

The combined observations of reef fishes in the Virgin Islands (Collette and Talbot 1972), the Great Barrier Reef, Australia (Domm and Domm 1973), Hawaii (Hobson 1972), and the Gulf of California (Hobson 1968) indicate nearly identical time relationships of behavioral events during

the twilight transitional periods. This would be the predicted relationship since fish respond to specific intensities and spectral composition of light (Munz and McFarland 1973). The intensity and spectral composition of incident light at specific times relative to sunrise or sunset are identical each day, although they vary with time and season and with latitude. The amount of cloud cover and/or high mountainous terrain nearby, as in Kaneohe Bay and Kona, Hawaii (Hobson 1972) or Baja California (Hobson 1968), may shift the activity patterns to later in the morning, or earlier in the evening (i.e., shift the time relative to sunrise and/or sunset at which specific light levels occur). However, the basic relationships between behavior and twilight periods appear to hold.

Light meter readings recorded during the formation and break up of Hawaiian silverside schools are compared with those recorded for two other species of siversides in Table 1. The readings for all three species are not significantly different. Such light levels occur naturally when the sun is between $-5°$ and $-9°$ below the horizon during the periods of evening or morning twilight (Brown 1952). These data and the field observations reported here are also comparable to the light levels and the sun angles calculated from the data presented by Pavlov (1962) for another silverside, *Atherina mochon pontica*. Pavlov found that peak predator success occurred at light levels of approximately 0.01-108 foot candles corresponding to sun angles of $-9°$ to $+1°$ to the horizon (Brown 1952) (i.e., centered during the period of civil twilight).

These comparisons indicate that related species of silversides, which live in widely separate parts of the world, have similar visual thresholds and, perhaps, sensitivity. Munz and McFarland (1973) provided a synopsis of research, which has shown that many related species demonstrate a considerable diversity in their visual sensitivity. However, species, whether related or not, which occur in similar environments, appear to have similar thresholds and sensitivity. These relationships indicate that the above silverside species from various locations in the world may have very similar behavioral patterns and/or live in very similar physical and biological environments.

When light levels decrease in the evening, visual thresholds may be reached, making coordinated schooling movements impossible, or at least more difficult for the silversides. These thresholds may be reached at the time when cone vision shifts to rod vision (the Purkinje shift), neither cone nor rod vision being fully efficient (Munz and McFarland 1973). As school formation breaks down or increases, the silversides appear to be the most vulnerable to predatory attack. This vulnerability may be due to reduced visual sensitivity, leading to an inability to see their predators below them against a dark bottom or deep water (Hobson 1966, 1968) and react in time to avoid and escape from them (Dill 1972, 1974a, b). In addition, such prey may be unable to simultaneously interact with conspecifics, and look out for predators at a distance at low light levels.

Predators are presumably able to see their prey at a horizontal angle or silhouetted against the twilight sky for a short period of time before their lower visual threshold is reached in the evening (Hobson 1966, 1968). Munz and McFarland (1973) indicated that increased visual sensitivity in predators, which provides sufficient resolution for the detection of prey in motion during twilight, may be a result of having relatively larger, but fewer, cones in their retinas compared with those found in diurnal fishes. This factor is critical since predators must align themselves and be able to predict where their prey will be during the mouth opening phase of their strike (Nyberg 1971).

Weighing against the hypothesis that the schools of silversides break up and reform as a result of changes in visual sensitivity, are a number of observations made of captives held in the field enclosures in the absence of predators. When held for weeks at a time, these silversides did not completely lose their cohesion and polarity, indicating that there may be a strong genetic component to their schooling behavior. This genetic component may result in the silversides remaining within a short distance of one another at all times. The silversides appear to be adapted to feeding at night as well as in the day (McMahon 1975). If they can feed at night, the silverside are probably able to detect the presence of conspecifics, either using visual and/or lateral line cues. The ability to detect conspecifics would be particularly beneficial as individuals would not become so widely scattered during the night that polarized schools could not easily reform during morning twilight. In addition, the observation that captive silversides held in large enclosures in the field in the absence of predators did not all spread out to look continuously for food indicates

that there may be a biological (circadian) rhythm related to school formation and breakup and the availability of specific food resources. Thus, the breakup of schools may reflect a preemptory predilection of individual silversides to spread out and feed rather than remain within the safety of compact polarized schools. Concurrently, predators are rapidly losing their ability to distinguish individual silversides in the fading light, but their presence remains a threat.

During the morning the process is reversed as light levels increase with predators becoming increasingly active and presumably more successful at capturing silversides. It is during relatively short daily time spans within the periods of twilight that the silversides become particularly vulnerable to certain predators. It is at these times that the silversides are passing to or from a period of feeding to a period of relative quiescence. In some areas, exposure to predators may be increased because the transition involves the movement from one location to another. The timing of such movements and the behavioral changes that occur within schools appear to be related to the threat of predation, the availability of food and the visual sensitivity and thresholds of both the silversides and their predators.

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FISHES, MACROINVERTEBRATES, AND THEIR ECOLOGICAL INTERRELATIONSHIPS WITH A CALICO SCALLOP BED OFF NORTH CAROLINA

FRANK J. SCHWARTZ AND HUGH J. PORTER[1]

ABSTRACT

A 1972 study documented the fishery, fish and macroinvertebrate faunas, possible predators, and the ecological interrelationships of the offshore North Carolina calico scallop, *Argopecten gibbus*, bed(s). Environmental data of water temperature, salinities, chlorophyll a, water current direction, sediment grain size, and organic composition were obtained aboard commercial and chartered research vessels. Water temperatures progressed seasonally from 12° to 26° C while bottom salinities varied between 31 and 37‰ yet were not radically different from the surrounding habitats. Chlorophyll a data suggested a fairly stable but low plankton fauna over the bed(s) except for June and late October. Little or no differences in bottom type within or without the bed(s) were noted on the basis of sediment particle size, grain size, skewness, or sorting coefficients. Scallops grew faster in the experimental bed than in the commercial bed but little could be found to account for their differences in size. Some 111 species of fishes were captured over the bed(s). Of a vast moving fish fauna, 33 species dominated the catches. Of 46 species with food in their stomachs, 20.4% feed on scallops with only 9 species considered scallop predators. Bothids, soleids, rajids, labrids, dasyatids, and myliobatids were not active scallop predators. *Halichoeres caudalis* appeared in October when the fishery collapsed economically. Of 12 species of echinoderms, the sea stars *Luidia clathrata* and *Astropecten articulatus* were active scallop predators. While less abundant, 21 additional invertebrates were also suspected predators. *Luidia clathrata* and *A. articulatus* abundance on the beds remained high throughout the season; however, abundance off the beds was somewhat lower. No one factor has yet been found that made the North Carolina calico scallop beds unique, why they existed, or were productive in 1972.

Three commercial species of scallops occur in North Carolina: the Atlantic deepwater scallop, *Placopecten magellanicus* (Gmelin), the shallower offshore calico scallop, *Argopecten gibbus* (Linné), and the inshore bay scallop, *Argopecten irradians* (Lamarck). The offshore calico scallop fishery, while yielding varying quantities of harvestable scallops (Table 1), has alternately experienced good and bad years of production (Lyles 1969; Cummins 1971; Chestnut and Davis 1975). The disappearance of calico scallops from an area, whether off North Carolina, Florida, or elsewhere, is common knowledge (Bullis and Ingle 1959; Hulings 1961; Anonymous 1962; Kirby-Smith 1970; Roe et al. 1971; Porter and Wolfe 1972). Off North Carolina the causes of scallop fluctuations and production have been attributed to mortalities, migration, poor larval transport from elsewhere, introduction of scallop shucking and eviscerating machines, or overfishing (Webb and Thomas 1968; Lyles 1969; Cummins and Rivers 1970; Kirby-Smith 1970; Cummins 1971; Allen and Costello 1972). This report documents the fish and macroinvertebrate faunas, possible predators, and their ecological interrelationships with the scallop bed(s) that supported the 1972 fishery.

TABLE 1.—North Carolina calico scallop production, 1959-75.[1]
[No production 1962-64, 1968-69, and 1974-75.]

Year	Meats (pounds)	Value (dollars)	Gear
1959	6,572	2,629	Dredge
1960	111,726	44,691	Trawl
1961	22,427	8,971	Trawl
1965	871,100	244,709	Trawl
1966	1,856,760	368,685	Trawl
1967	1,388,606	306,843	Trawl
1970	1,574,087	498,570	Trawl
1971	1,285,304	432,025	Trawl
1972	1,050,320	492,899	Trawl
1973	556,315	353,757	Trawl

[1]Data supplied by the National Marine Fisheries Service Statistical Office, Beaufort, N.C., and Chestnut and Davis 1975.

NORTH CAROLINA CALICO SCALLOP FISHERY

While *A. gibbus* occurs in the western North Atlantic from the northern side of the Greater Antilles and throughout the Gulf of Mexico to

[1]Institute of Marine Sciences, University of North Carolina, Morehead City, NC 28557.

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Bermuda and possibly Delaware Bay (Waller 1969; Allen and Costello 1972), only three areas produce calico scallops of commercially harvestable quantities: North Carolina, Cape Canaveral off eastern Florida, and the Gulf of Mexico off Apalachicola Bay, Fla. (Drummond 1969; Cummins 1971; E. Willis pers. commun.). Throughout its range it has been found in depths of 2-370 m (Waller 1969). Off North Carolina, calico scallops occur at open water depths of 13-94 m (Cummins et al. 1962; Bullis and Thompson 1965; Porter 1971, 1972a; Allen and Costello 1972).

Until recently, North Carolina calico scallops were hand shucked by shore-based operations (Cummins 1971). In 1970, two shucking machines (Webb and Thomas 1968) were introduced in North Carolina and by 1975 there were eight. The present North Carolina and Florida fisheries prefer this shucking method rather than utilizing offshore vessels equipped with machine shuckers, as was briefly used off Florida (Allen and Costello 1972). Generally, commercial fishing is considered feasible when 20 bushels (in shell) are caught per hour with shell diameter of at least 40 mm (Drummond 1969). Meat size to be acceptable to hand shucking should be 190 meats/kg or 90 meats/pound (Cummins 1971). Machine processed meats can be as small as 495 meats/kg (225 meats/pound).

Off North Carolina, the high cost of hand shucking and the early lack of knowledge concerning a possible calico scallop fishery delayed its development (Chestnut 1951). The fishery seems to have begun in 1959 and has since been described by Cummins et al. (1962), Cummins (1971), Porter (1971, 1972a), and Porter and Wolfe (1972). At first scallop dredges were used to harvest calico scallops. Today, otter trawls are the gear used by the commercial fishery (Rivers 1962). Short tows of 10-15 min often land 60 or more bushels, with an average day's catch being 800-1,500 bushels of shell stock.

STUDY AREA

Cummins et al. (1962) characterized the principal North Carolina calico scallop grounds as an elliptical shaped bed 16 km long near Cape Lookout, with several lesser beds located in 19-37 m depths northeast and southeast of the Cape. The major North Carolina calico scallop fishery in 1971 was located southeast of Cape Lookout; a small bed southeast of the Cape was also fished briefly in September of that year. Exploratory efforts in 1972 by the commercial fleet and the RV *Dan Moore* on the beds southwest of New River and northeast of Cape Lookout (Figure 1) failed to locate commercial quantities of calico scallops. The only beds that supported the 1972 fleet of 13 vessels from February to October were located 16-24 km south of Beaufort, N.C., producing some 1 million pounds of meats (Table 2).

The 1972 study area consisted of the above beds located at lat. 33°35′N between long. 76°35′ and 76°55′W (Figure 2). Depths were 20-25 m and most sampling occurred inside the 28-m contour.

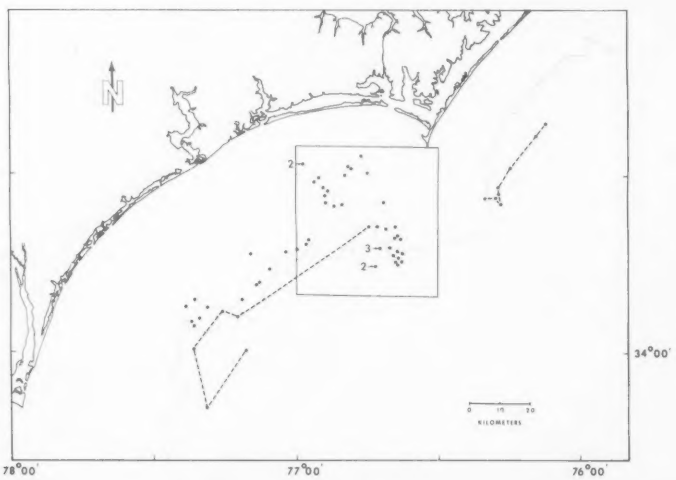

FIGURE 1.—North Carolina calico scallop fishing grounds. Dots refer to areas of poor catch by commercial fishermen during the 1972 season. Dashed lines indicate exploratory trips by one or more trawlers. Solid line refers to the area contained in Figure 2. Dotted line indicates 20-fathom (36.6-m) contour.

TABLE 2.—North Carolina calico scallop production, 1972.[1]
[No production in November and December.]

Month	Pounds	Value ($)	Month	Pounds	Value ($)
Jan.	2,800	1,624	July	68,768	46,763
Feb.	24,064	9,626	Aug.	43,624	35,772
Mar.	184,688	72,028	Sept.	33,008	29,047
Apr.	280,800	101,087	Oct.	544	478
May	228,400	93,644	Total	1,050,320	492,899
June	183,624	102,830			

[1]Data supplied by the National Marine Fisheries Service Statistical Office, Beaufort, N.C., and Chestnut and Davis 1975.

METHODS

Sampling Vessels

Two types of vessels were used to sample the offshore North Carolina calico scallop beds. Commercial fishing vessels, from which most of the samples were obtained, were the 25-m MV *Ensign*, a side trawler of Gloucester design and the 15-m MV *Seven Brothers*, a double rigged shrimper design. Research vessels include the RV *Beveridge*, a 17-m shrimp trawler which was chartered monthly to collect additional samples or to maintain anchored equipment, and the Duke University 33-m RV *Eastward*, a side trawler of Gloucester design. One bottom observational cruise was accomplished by using RUFAS (Anonymous 1969) aboard NOAA RV *George M. Bowers*. Two additional samples, 23 April and 27 June, were also obtained while returning from other *Eastward* projects.

All commercial or chartered vessels towed one or two 10-12 m scallop trawls (Rivers 1962) which were modified to have heavily weighted foot lines and heavy-duty chaff gear on the cod end. The trawl on the *Beveridge* was rigged the same as that of the commercial vessels except that the foot line was the standard weighted loop chain design preceded by a light tickler chain. Mesh size of all trawls was the standard flat shrimp type. Sampling tow interval varied on the commercial vessels by season as a function of scallop abundance. *Beveridge* or *Eastward* tows were kept to 15 min. Sample tow distances, by commercial vessels, varied ¼-½ km, whereas *Beveridge* and *Eastward* tows were ¼ km. No effort, by type of vessel, was made to sample with or against the current.

Environmental Data

Water temperatures were obtained with a mercury thermometer immersed in bottom water obtained by a 3.1-liter Kemmerer sampler.

Salinities were determined from the water sample by using a direct reading American Optical Corp.[2] refractiometer.

Chlorophyll a was determined spectrophotometrically for 19 stations (Figure 2) following the methods of Strickland and Parsons (1968) and expressed as milligrams per cubic meter.

A Braincon 381 current meter was anchored and buoyed at the northwestern edge of the commercial grounds. Excessive fouling during much of the sample year by hydroids, sponges, and tunicates prevented precise long-term bottom current data being recorded at the surface of the bed. After rebouying the meter to record currents 30 cm above the bed, current data obtained over a 26-day period, mid-August to mid-September, indicated a northeastward current drift component (Schumacker 1974).

Sediment samples taken by Peterson (*Beveridge*) and Shipek (*Eastward*) grabs (Figure 3) were frozen until grain size and organic determinations could be made. Pretreatment for grain-size analysis included washing each sample in a large volume of fresh water and then decanting after all sediment had settled. Washing was done to reduce weighing errors induced by salt crystals. Following decanting, sediments were oven dried at 85°C and separated into sediment sizes by a U.S. Standard Sieve Series and mechanical sieve shaker. All samples were in the shaker for at least 2 h. Analysis of data followed Morgans (1956).

Percent organic material was determined from 1 to 2 g unwashed subsamples which had been oven dried for 48 h at 85°C. The amount of organics was assumed to be the difference in sample weights before and after firing at 500°C for 2 h. This followed a technique used in the Marine Sediments Laboratories of Oregon State University (J. Paul Dauphin pers. commun.).

An attempt was made to develop a fast method for percent organic determinations of marine sediments through the manufacturer's suggested use of a Coleman Model 33 Carbon-Hydrogen Analyzer, rented from the Duke University Marine Laboratory. Comparison of data, by statistical means, showed no correlation between analyzer and ovenfired organic values from offshore marine sediments.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

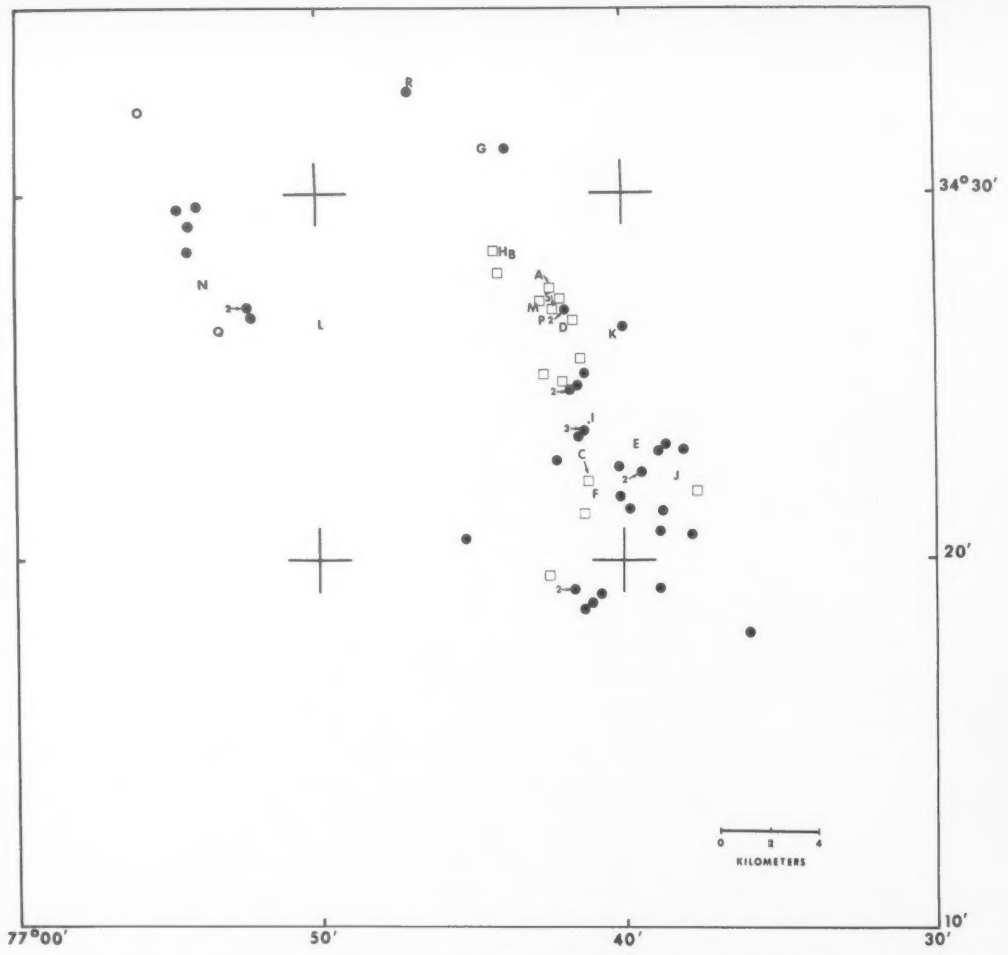

FIGURE 2.—North Carolina calico scallop fishing grounds. Dots refer to known locations of good catches by commercial trawlers. Open squares refer to known locations of good catch by RV *Beveridge*. Letters refer to chlorophyll a sampling stations. For location of enclosed area off North Carolina coast see Figure 1.

Fishes

Fishes of at least 100 mm standard length were tagged using 12-mm Peterson disk tags held in place (in the middorsolateral musculature) by Monel pins. Fish lengths, except for skates and stingrays where wing width was used, were expressed for each species and specimen as standard length. Once tagged, release was immediate over the original collecting site. The ship's loran was used to pinpoint the release site. Other biological data were taken on those additional fishes that had not been too badly damaged by the fishery or scallop catches. Notations of other fishes not captured, such as flyingfishes, completed the field data.

Fish samples from commercial catches and destined for stomach content analyses were kept on ice because of the danger of Formalin contamination of the scallop catch and the cramped ship quarters prevented carrying extra gear afield. Similar fish sampled aboard research vessels were preserved in 20% Formalin. In the laboratory, the entire digestive tract was removed, contents identified, and noted whether the food items were in the stomach or intestine. Positive identification of

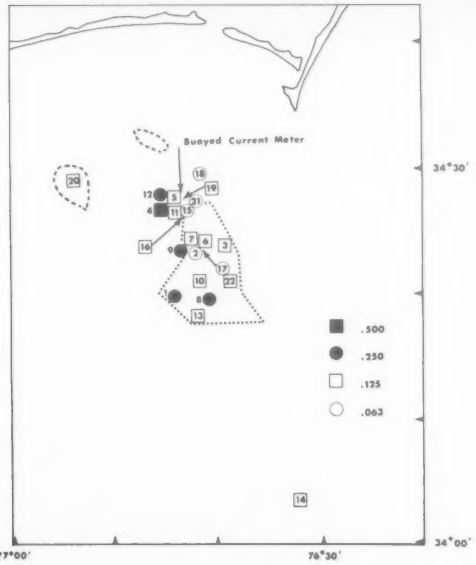

FIGURE 3.—Twenty-two sediment sample stations. Dominant grain size is indicated by station. Broken lines enclose the commercial area, an area fished by the calico scallop fishery.

the food items to species was possible in most cases.

Scallops

Scallops were sampled from two areas—one general and one specific. The general area, hereafter referred to as the commercial area, included wherever the scallop fishery was operating (Figures 1-4). Scallop tissue samples from this area were taken, when possible, once a week; shell length measurements and other appropriate scallop data were taken more frequently. Tissue, gonad and/or spawning condition data will be covered in a paper by Porter and Schwartz (in prep.).

The specific area, hereafter referred to as the experimental area, was an area just northwest of the commercial area. This area was sampled monthly by the *Beveridge* and was marked from June to September 1972 by a large red buoy; this buoy further served to support the Braincon current meter (Figure 3). The seabed interval between this area and the commercial area to the south contained no scallops, which suggested that this area was a small separate bed. Only briefly during the latter part of the commercial scallop season was the experimental area worked by the 1972 fishery.

Sea Stars

Data were accumulated on seasonal distribution of the sea stars present on the scallop beds, their size, and relative abundance. Sea star size is here defined as the radius of a sea star through its longest arm.

About 20 *Astropecten articulatus* and about 20 *Luidia clathrata* were examined weekly, when available, for stomach contents. *Luidia alternata*, *Goniaster americanus*, and *Echinaster brasiliensis* stomachs were also examined, when available. Stomach analysis examinations which also delineated associated organisms were similar to those of Porter (1972b) and will be reported on elsewhere.

Associated Macroinvertebrates

Unculled bushels of scallops, as caught by the trawlers, were examined periodically by the field investigator to note other associated organisms, amount of shell material, and signs of dead or dying scallops. Counts were made of each organism and the amount of dead shell or trash. A log was also kept of all macroinvertebrate species seen during each cruise.

ENVIRONMENTAL OBSERVATIONS

Bottom water temperatures exhibited a natural progression from about 12°C in February to a high near 26°C in September. These were within the range 9.9°-33°C noted by Waller (1969). Vernberg and Vernberg (1970), in laboratory experiments of North Carolina calico scallops, found none survived after 48 h exposure to water of 10°C.

Bottom salinities throughout the bed, as evidenced during the shifting seasonal fishing effort (Figure 4), remained fairly constant at 35‰ (range 31-37‰, Figure 5). This agreed with observations of others for scallop grounds elsewhere (Anderson et al. 1961; Hulings 1961; Grassle 1967; Pequegnat and Pequegnat[3]).

Kirby-Smith (1970) and Allen and Costello (1972) suggested that upwelling in the vicinity of

[3]Pequegnat, W. E., and L. H. Pequegnat. 1968. Ecological aspects of marine fouling in the northeastern Gulf of Mexico. Texas A&M Univ. Dep. Oceanogr. Proj. 286-F, Ref. 68-22T, 80 p.

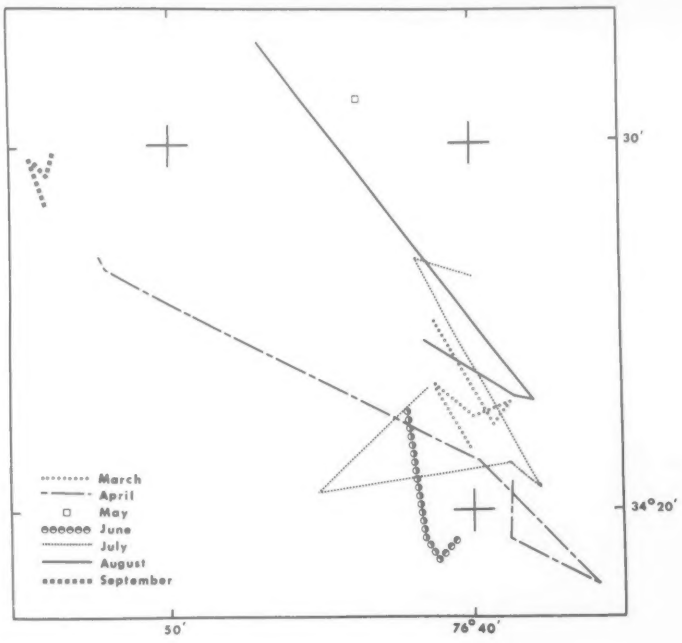

FIGURE 4.—Areas fished by commercial fishery during the 1972 season. Locations taken from ship's log.

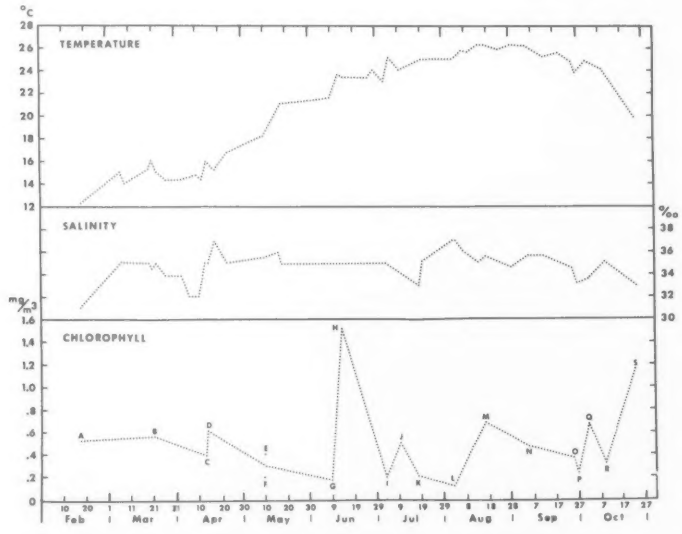

FIGURE 5.—Environmental data collected from the calico scallop grounds. Each data point for water and salinity indicates individual date sampled. Letters on chlorophyll graph refer to station sampled that date, see Figure 2 for locations.

Cape Lookout (Taylor and Stewart 1959; Wells and Gray 1960; Gaul et al.[4]) may produce high plankton concentrations and that these concentrations may occur where scallop abundance is greatest. Chlorophyll a analyses during 1972 (Anonymous[5]) suggested that a fairly stable but

[4]Gaul, R. D., R. E. Boykin, and D.E. Letzring. 1966. Northeast Gulf of Mexico hydrographic survey data collected in 1965. Texas A&M Univ. Dep. Oceanogr. Proj. 286-D, Ref. 66-8T, 202 p.

[5]Anonymous. 1972. Data report for R/V *Eastward* cruise E-12-72, July 3-8, 1972. Duke Univ. Mar. Lab., Beaufort, N.C., 34 p.

low plankton fauna existed over the scallop beds, except during June and late October, when indications of a late spring and early fall bloom occurred (Figure 5).

Twenty-two sediment samples were taken during the 1972 study (Figure 3). Of these, seven were deliberately taken in areas where no scallops were collected by the fishery (Table 3). As the sediments were taken immediately after a trawl tow, they may not be representative of the same bottom covered during the tow. No discernible differences were found between sediments from scallop producing and nonproducing areas (Table 3, Figure 2).

Newton et al. (1971, Sediment Distribution Chart No. 2) characterized the area which was later encompassed by the 1972 commercial scallop fishery (Figures 3, 4) as consisting of two sediment

TABLE 3.—Sediment size analyses, data listed as percent per sample, sediment sorting coefficients, skewness, for scallops sampled in 1972 from producing and nonproducing areas off North Carolina.

Sediment size (mm)	Sediment sample station and sample date						
	1	2		3	4	5	6	7
	18 Feb.	18 Feb.		18 Feb.	18 Feb.	21 Mar.	21 Mar.	21 Mar.
>4	0.572	0.701	1.031	0.102		0.072	0.406	0.0027
2-4	1.734	0.381	0.626	0.165	18.235	0.362	0.381	0.0068
1-2	8.289	1.530	2.715	0.573	22.831	0.651	0.964	0.0139
0.5-1	32.299	2.325	3.903	2.090	25.053	1.505	2.224	0.0303
0.250-0.5	40.606	3.898	5.842	34.711	19.814	13.576	12.670	0.1443
0.125-0.250	13.847	14.748	14.649	49.834	7.782	81.622	40.021	0.2982
0.063-0.125	1.826	69.186	64.396	9.836	3.431	0.001	40.096	0.4646
<0.063	0.826	7.231	6.837	2.688	2.855	2.211	3.239	0.0392
Median particle size[1]	1.17	3.37	3.32	2.22	0.35	2.42	2.80	3.02
Median particle size (mm)	0.44	0.09	0.09	0.21	0.77	0.17	0.14	0.12
Sediment sorting coef[1]	0.675	0.365	0.485	0.555	1.100	0.300	0.635	0.685
Sediment skewness[1]	−0.045	0.015	−0.105	−0.035	0.	−0.020	0.035	−0.155
Percent organic	2.027	1.080		0.844	2.118	0.884	0.790	1.394
Latitude N	34°22'	34°24'		34°24'	34°26.5'	34°27'	34°24'	34°24'
Longitude W	76°44'	76°42'		76°39'	76°45'	76°44'	76°41'	76°42.5'
Depth (m)	25	24		24	22	22	24	25
Scallop producing area	no	yes		no	yes	no	yes	yes

Sediment size (mm)	8	9	10	11		12	13	14
	21 Mar.	21 Mar.	10 May	14 June		14 June	14 June	25 June
>4	0.0019	0.0313		8.026	3.640	0.491	0.012	0.064
2-4	0.0196	0.0347	0.341	8.118	3.855	1.088	0.339	0.074
1-2	0.0595	0.0643	1.062	8.102	7.438	3.318	1.084	0.890
0.5-1	0.2356	0.2678	2.769	19.210	19.475	9.113	5.071	3.936
0.250-0.5	0.5574	0.4873	11.619	2.623	2.810	44.895	27.046	30.632
0.125-0.250	0.1132	0.0854	44.095	28.842	40.369	6.080	61.209	62.931
0.063-0.125	0.0096	0.0207	31.974	13.432	16.683	30.813	5.218	1.231
<0.063	0.0032	0.0085	8.139	11.647	5.730	4.201	0.022	0.242
Median particle size[1]	1.33	1.22	2.78	2.13	2.32	1.80	2.27	1.23
Median particle size (mm)	0.39	0.42	0.14	0.22	0.18	0.28	0.20	0.41
Sediment sorting coef[1]	0.525	0.645	0.650	1.465	1.215	1.060	0.505	0.480
Sediment skewness[1]	−0.085	−0.145	0.070	−0.615	−0.605	0.500	−0.095	−0.090
Percent organic	2.176	2.461	ND[2]	1.638		0.885	0.763	0.840
Latitude N	34°19.5'	34°23.5'	34°21'	34°27'		34°27.5'	34°18.5'	34°3.4'
Longitude W	76°41'	76°43.5'	76°41.5'	76°44'		76°45'	76°42'	76°32.7'
Depth (m)	28	23	26	23		21	29	37
Scallop producing area	yes	yes	yes	no		no	yes	no

Sediment size (mm)	15	16	17	18	19	20	21	22
	27 June	17 Aug.	17 Aug.	17 Aug.	12 Sept.	12 Sept.	23 Oct.	23 Oct.
>4	1.082	0.021	0.044	0.000	0.049	0.000	0.665	0.243
2-4	1.016	0.437	0.146	0.234	0.363	0.001	0.480	0.446
1-2	1.472	1.556	0.756	0.603	1.043	0.007	1.386	1.162
0.5-1	2.573	3.345	2.472	2.646	2.103	0.026	2.515	2.821
0.250-0.5	5.800	24.389	6.758	8.376	6.175	0.209	6.451	11.387
0.125-0.250	14.705	58.881	20.293	23.028	62.728	0.638	20.518	46.534
0.063-0.125	66.049	9.525	62.619	59.094	26.885	0.097	62.462	35.038
<0.063	7.304	1.847	6.912	6.019	0.654	0.022	5.523	2.370
Median particle size[1]	3.35	2.36	3.32	3.26	2.65	2.38	3.27	2.72
Median particle size (mm)	0.09	0.19	0.10	0.10	0.15	0.19	0.10	0.15
Sediment sorting coef[1]	0.425	0.485	0.500	0.555	0.465	0.380	0.505	0.585
Sediment skewness[1]	−0.055	−0.075	−0.100	−0.135	0.065	0.020	−0.095	0.090
Percent organic	0.967	1.151	0.866	1.037	0.593	1.251	1.021	1.119
Latitude N	34°26.3'	34°26'	34°23.5'	34°29.5'	34°27'	34°29'	34°27'	34°21'
Longitude W	76°43'	76°43'	76°41'	76°41.5'	76°42.5'	76°54'	76°42'	76°38.5'
Depth (m)	18	22	23	19	21	20	21	26
Scallop producing area	yes?	yes	yes	no	yes?	yes	yes	yes

[1]See Morgans (1956) for definition.
[2]Not determined.

types, most of the bed being "fine sand - grey" while areas of its western edge were "shell hash - often brown - many types of organic contributors." The latter was typical of our sediment sample 14. The area from which sediment sample 20 was taken was characterized as "Coarse sand - very shelly - iron stained"; the experimental area northwest of the main scallop producing area was characterized as "fine sand - iron stained - less than 25% shell material." Median grain size analyses of our data agreed with Newton et al. (1971) in that parts of the western edge of the calico scallop bed had coarser sediments than other areas encompassed by the main bed (Figure 3); however, no differences were found between the main scalloping area, the experimental area north of the bed, and stations 14 and 20.

Sanders (1958) and Bloom et al. (1972) suggested that optimal sediment conditions for filter feeders were a fine (about 0.18 mm) and a well-sorted, but positively skewed, grain size. Median sediment sizes found within the 1972 North Carolina calico scallop bed averaged below Sanders' 0.18 mm optimal size for filter feeders. Subsequent to this study, plotting the location of the 1973 calico scallop fishery off the North Carolina coast on the Newton et al. (1971) sediment chart, revealed that the 1973 fishery was in an area not of fine sand but very coarse shelly sand. This has been further corroborated by personal observations aboard vessels in the fishery. These data may support the contention of McNulty et al. (1962) that other factors besides grain size are important to the well being of filter feeders.

Sorting coefficient values for most sediment samples ranged from 0.300 to 0.685 (Table 3, a condition considered well sorted), although two samples located northwest of the main fishery had relatively high sorting coefficients (1.100 to 1.465). Sediments in these same two samples were also strongly skewed (−0.615 and 0.500, Table 3). While sorting coefficient values agreed with the conclusions of Sanders (1958) and Bloom et al. (1972), the sediment skewness data did not. Most of the data was only slightly skewed (−0.155 to 0.090) and not strongly positively skewed as they suggested.

Commercial fishermen reported that there were numerous rough areas, including a small low ledge, outside the commercial area which caused great damage to their nets. Porter and Wolfe (1972) described the North Carolina scallop grounds as consisting of sand, shell fragments, and occasionally large pieces of trent marl and coquina. Porter and Wolfe (1972) and Pearse and Williams (1951) described a small bed southwest of New River which was surrounded by bottom containing large heads of lobe star coral, *Solenastrea hyades* (Dana). During 1972, large masses of trent marl were not infrequently brought up in the scallop nets by the commercial fishermen. Ledgelike outcroppings of marl (?) and large heads of the lobe star coral outside the commercial area were observed in 1972 while aboard the *George M. Bowers* through use of its remote underwater television sled RUFAS. While such marl outcrops and coral heads are not uncommon throughout the southern North Carolinian coastal area, known calico scallop beds do not seem to be dependent upon their presence.

CALICO SCALLOP GROWTH

Length measurements were taken on 5,180 scallops during the sampling period (Table 4). Scallop (865) mean growth in the experimental area was faster than that from the commercial area (Table 4); size increase over a 7-mo sampling period was 17.8 mm or 2.5 mm/mo. Comparable growth data obtained from 4,315 scallops landed by the commercial fishery over the 9-mo sampling period were 8.7 mm or 1.1 mm/mo; their sizes ranged from 35 to 65 mm with no live small scallops being noted. The difference in rate of growth was probably related to the original smaller size of the experimental area scallops, which ranged from 28 to 57 mm in length (Table 4). Allen and Costello (1972), reviewing the calico scallop literature, noted growth data of 4.0 mm/mo for scallops having mean sizes of 13.9 to 37.8 mm and 0.3 mm/mo for scallops having mean sizes of 75 to 80 mm.

As mentioned above, the scallops from the ex-

TABLE 4.—Lengths (millimeters) of calico scallops collected monthly from the experimental bed north of the main bed and commercial catch, 1972.

	Experimental bed			Commercial catch		
Month	Average length	Size range	Sample size	Average length	Size range	Sample size
Feb.	35.5	28-44	100	47.3	40-54	545
Mar.	37.4	30-47	150	46.3	37-55	510
Apr.	—	—	—	47.3	35-56	617
May	49.8	43-55	86	47.8	41-62	276
June	44.8	33-54	152	50.7	39-70	1,100
July	—	—	—	47.6	35-61	450
Aug.	45.0	39-57	127	50.8	36-59	400
Sept.	53.3	44-64	150	54.2	48-65	316
Oct.	50.5	42-57	100	55.0	43-65	101
Average length increase	17.8			8.7		

perimental area were consistently smaller than those from the commercial area (Table 4). Median sediment size and texture analyses data from the two areas were virtually identical (Table 3). There was some indication that organic values in the experimental area may be slightly higher than those from the commercial area (Table 3). Carriker (1959) noted that growth of *Mercenaria mercenaria* was faster in his low organic areas than in areas with higher organic percentages. This was the opposite of our findings.

Apparently the growth of the calico scallop is not related to chlorophyll a content for we noted primarily little difference between chlorophyll a content, regardless of sampling area (Figure 5).

FISHES OF THE CALICO SCALLOP BED

Some 4,461 fishes belonging to 49 families and 111 species were collected during the 51 cruises between 9 January and 23 October 1972. One additional species, *Scorpaena isthmensis,* was added to the faunal list during exploratory trips in 1971 and 1973. Pelagic, demersal, and benthic families and species were represented in the catches (Table 5). Of the total fishes landed (4,392) as part of the 1972 scallop catches, 985 were tagged and released to note movements, 1,655 were analyzed for food content, and 1,752 specimens were merely observed and identified. Most of the 112 species encountered were sporadic components of the scallop bed either as they passed north-to-south or east-to-west, depending on the season of the year.

Of the 112 species of fishes associated with the calico scallop bed, 94 or 84.0% can be considered Caribbean in their main distribution and abundance, while 7 (6.2%) were Virginian forms that had moved seasonally south of the Cape Hatteras barrier. Eleven species (9.8%) were those whose distribution ranges extended naturally over a broad north-south geographic area and could not be considered northern or southern faunal components. Controversy still exists whether that portion of the shelf off North Carolina is simply a part of an overall north-south temperate Virginia Province faunal region (Forbes 1856) or an area divided into a nearshore Virginia and offshore Gulf Stream influenced Carolinian Province (Gray and Cerame-Vivas 1963; Wells et al. 1964; Cerame-Vivas and Gray 1966; Gray et al. 1968; Bumpus 1973; Briggs 1974). Struhsaker (1969) and Schwartz (in press) have shown this area to be rich in fishes with an overall 70:30 ratio of southern to northern fishes, a condition far richer than that of the northern Gulf of Mexico, contrary to the findings of Briggs (1974).

Some 33 species dominated the 1972 catches, of which 21 species accounted for 77.1% of the fishes handled: *Stenotomus aculeatus* (413 specimens), *Synodus foetens* (386), *Paralichthys dentatus* (303), *Diplectrum formosum* (254), *Raja eglanteria* (252), *Orthopristes chrysopterus* (249), *Prionotus scitulus* (196), *Monacanthus hispidus* (174), *Centropristes striata* (122), *Balistes capriscus* (120), *Prionotus evolans* (116), *Hemipteronotus novacula* (104), *Leiostomus xanthurus* (104), *Mustelus canis* (95), *Lagodon rhomboides* (91), *Aluterus schoepfi* (85), *Paralichthys albigutta* (77), *Etrumeus teres* (75), *Urophycis regius* (74), *Syacium papillosum* (73), and *Ancylopsetta quadrocellata* (71).

A few species, notably *Raja eglanteria, Centropristes striata, Ancylopsetta quadrocellata,* and *Paralichthys dentatus,* seemed to occupy the beds throughout the year (Table 5). The loss of such species as *Prionotus evolans, Orthopristes chrysopterus,* and *Aluterus schoepfi* from the beds was evident as they moved shoreward during the summer months. *Mustelus canis* and *Urophycis regius* were winter components of the fauna prior to their movement northward or seaward away from the encroaching higher summer water temperatures. Others, such as *Diplectrum formosum, Mullus auratus,* and *Aluterus scriptus* occurred during or appeared late in the summer, apparently transported by meanders of the Gulf Stream (Webster 1961; Roe et al. 1971) from the south when water conditions met their usual tropical temperature requirements for existence. *Rhinoptera bonasus* was a good sample of a north-south transient in April and August as the schools moved past the area to other grounds (Schwartz 1965). *Halieutichthys* was an example of an offshore species apparently moving into shallower water with occasional incursions (Blanton 1971) of deep ocean water onto the shelf. As expected, bottom fishes of the families Bothidae, Soleidae, Triglidae, and hard shell crushers of the Balistidae and Tetraodontidae predominated (Table 5). The most exciting captures were *Letharchus velifer, Seraniculus pumilio, Prionotus ophryas,* and *Scorpaena isthmensis,* as their capture represented sizeable northward range extensions. McEachran and Eschmeyer (1973) have also recently noted the northward extension of *S. isthmensis.*

Nineteen species were tagged for movement

TABLE 5.—A list of fish species encountered during the various calico
T = tagged; F = food analysis; A = additional

Species	1971	Jan.-Feb.			March			April			May			June		
		T	F	A	T	F	A	T	F	A	T	F	A	T	F	A
Carcharhinus obscurus		—	—	—	—	—	—	1	—	—	—	—	—	—	1	—
Mustelus canis		6	3	20	21	7	—	14	23	1	—	—	—	—	—	—
Rhizoprinodon terraenovae		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Squalus acanthias		—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Squatina dumerili		—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
Rhinobatos lentiginosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Narcine brasiliensis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Raja eglanteria		—	1	11	30	114	12	9	8	2	14	—	—	12	1	—
Dasyatis americana		—	—	—	—	—	—	5	1	1	—	—	—	1	—	—
D. centroura		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gymnura micrura		—	—	—	1	—	—	2	1	—	—	—	—	—	—	—
Myliobatis freminvillei		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Rhinoptera bonasus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Manta birostris		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gymnothorax nigromarginatus saxicola		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Conger oceanicus		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Letharchus velifer		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ophichthus ocellatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etrumeus teres		—	—	—	—	—	60	—	—	—	—	—	15	—	—	—
Anchoa hepsetus		—	—	—	—	—	—	—	—	57	—	—	—	—	—	—
Synodus foetens		—	1	13	6	75	70	—	—	16	9	47	10	—	2	—
S. poeyi		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trachinocephalus myops	4	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Opsanus tau		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Porichthys porosissimus		—	—	—	—	3	—	—	—	—	—	1	—	—	—	—
Gobiesox strumosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lophius americanus		—	—	—	—	2	—	—	1	—	—	—	—	—	—	—
Antennarius ocellatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. scaber	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halieutichthys aculeatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ogcocephalus sp.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Urophycis earli		—	—	—	—	—	—	—	—	3	—	—	—	—	—	—
U. regius	1	—	1	2	—	—	54	2	3	12	—	—	—	—	—	—
Rissola marginata		—	—	—	—	—	—	—	—	10	—	—	—	—	—	—
Fistularia tabacaria	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus erectus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Syngnathus springeri	3	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Centropristes ocyurus		—	—	15	—	—	—	—	—	—	1	2	—	5	—	—
C. philadelphicus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. striatus	11	—	2	2	—	—	—	10	7	2	14	5	—	11	6	—
Diplectrum formosum	3	—	—	—	—	—	—	—	—	—	3	1	—	11	52	—
Serranus phoebe		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. subligarius		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Serraniculus pumilio		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rypticus maculatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pristigenys alta	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pomatomus saltatrix		—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Caranx fusus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Decapterus punctatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lutjanus vivanus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haemulon aurolineatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. plumieri		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Orthopristis chrysopterus		—	7	23	1	5	2	4	11	151	16	21	—	2	1	—
Archosargus probatocephalus		—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Calamus bajonado		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
C. leucosteus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lagodon rhomboides		—	10	75	—	—	—	—	—	5	—	—	—	—	—	—
Sparisoma radians		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stenotomus aculeatus		—	5	13	3	20	16	11	12	171	10	45	—	4	1	—
Cynoscion nebulosus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. regalis		—	—	6	—	—	—	—	—	—	—	—	—	—	—	—
Parequetus sp.	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Larimus fasciatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leiostomus xanthurus		—	3	10	—	—	—	—	1	—	—	1	—	—	—	—
Menticirrhus americanus		—	2	3	2	—	—	—	—	—	—	—	—	—	—	—
M. saxatilis		—	2	6	4	1	7	5	7	1	—	—	—	—	—	—
Micropogon undulatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mullus auratus	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetodipterus faber		—	—	—	1	—	—	—	—	—	3	1	—	—	—	—
Chromis enchrysurus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halichoeres bivittatus	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. caudalis	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemipteronotus novacula	17	—	—	—	—	3	3	1	1	—	—	4	5	6	11	—
Astroscopus y-graecum		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trichurus lepturus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euthynnus alletteratus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

scallop cruises aboard commercial, research, and chartered vessels.
species encountered but not examined or tagged.

Species	July			August			September			October			1972 total			Total 1972
	T	F	A	T	F	A	T	F	A	T	F	A	T	F	A	
Carcharhinus obscurus	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
Mustelus canis	—	—	—	—	—	—	—	—	—	—	—	—	41	33	21	95
Rhizoprinodon terraenovae	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Squalus acanthias	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Squatina dumerili	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
Rhinobatos lentiginosus	—	—	1	—	—	1	—	—	1	—	—	—	—	—	3	3
Narcine brasiliensis	—	—	1	1	—	1	—	—	—	—	—	—	1	—	2	3
Raja eglanteria	8	1	—	18	6	—	1	2	—	—	2	—	92	135	25	252
Dasyatis americana	—	—	—	—	—	—	—	—	—	—	—	—	6	1	1	8
D. centroura	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Gymnura micrura	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	4
Myliobatis freminvillei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Rhinoptera bonasus	1	—	1	4	—	—	—	—	—	—	—	3	5	—	4	9
Manta birostris	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Gymnothorax nigromarginatus saxicola	—	—	—	—	—	—	—	1	1	—	—	—	—	1	1	2
Conger oceanicus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Letharchus velifer	—	—	—	—	—	1	—	—	1	—	—	—	—	—	2	2
Ophichthus ocellatus	—	—	—	—	—	—	—	—	1	—	—	1	—	—	2	2
Etrumeus teres	—	—	—	—	—	—	—	—	—	—	—	—	—	—	75	75
Anchoa hepsetus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57	57
Synodus foetens	—	4	—	—	54	32	—	12	5	—	5	25	15	200	171	386
S. poeyi	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Trachinocephalus myops	—	2	—	—	5	1	—	—	—	—	—	—	—	8	1	9
Opsanus tau	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1
Porichthys porosissimus	—	2	—	—	2	1	—	—	—	—	—	1	—	8	2	10
Gobiesox strumosus	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Lophius americanus	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3
Antennarius ocellatus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
A. scaber	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halieutichthys aculeatus	—	—	—	—	—	3	—	—	2	—	—	—	—	—	5	5
Ogcocephalus sp.	—	—	—	—	—	5	—	—	—	—	—	1	—	—	6	6
Urophycis earli	—	—	—	—	—	1	—	—	—	—	—	—	—	—	4	4
U. regius	—	—	—	—	—	—	—	—	—	—	—	—	2	4	68	74
Rissola marginata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	10
Fistularia tabacaria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippocampus erectus	—	—	—	—	—	2	—	—	1	—	—	—	—	—	3	3
Syngnathus springeri	—	—	1	—	—	1	—	—	1	—	—	—	—	—	5	5
Centropristes ocyurus	—	5	—	1	—	5	—	—	—	—	—	3	7	7	23	37
C. philadelphicus	—	—	3	—	—	3	—	—	4	—	—	1	—	—	11	11
C. striatus	2	4	—	12	7	1	6	19	—	2	7	3	57	57	8	122
Diplectrum formosum	2	11	4	—	3	27	—	—	73	—	—	67	16	67	171	254
Serranus phoebe	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
S. subligarius	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Serraniculus pumilio	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Rypticus maculatus	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2	2
Pristigenys alta	—	—	—	—	—	2	—	—	1	—	—	4	—	—	7	7
Pomatomus saltatrix	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Caranx fusus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Decapterus punctatus	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2	2
Lutjanus vivanus	—	—	—	—	—	—	—	—	1	—	—	2	—	—	3	3
Haemulon aurolineatus	—	—	—	—	—	2	—	—	3	—	—	1	—	—	6	6
H. plumieri	—	—	—	—	1	3	2	—	1	—	—	—	2	1	4	7
Orthopristis chrysopterus	—	—	—	—	—	—	1	—	—	2	2	—	26	47	176	249
Archosargus probatocephalus	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Calamus bajonado	—	—	—	1	—	—	—	—	—	—	—	—	1	—	1	2
C. leucosteus	—	—	—	2	4	1	2	11	—	—	—	—	4	15	1	20
Lagodon rhomboides	—	—	—	—	—	1	—	—	—	—	—	—	—	10	81	91
Sparisoma radians	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Stenotomus aculeatus	1	5	—	6	2	3	—	3	2	42	8	30	77	101	235	413
Cynoscion nebulosus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
C. regalis	—	—	—	—	—	—	—	—	—	—	—	2	—	—	8	8
Parequetus sp.	—	—	—	—	—	—	—	—	2	—	—	—	—	—	2	2
Larimus fasciatus	—	—	—	—	—	—	—	—	—	—	—	4	—	—	4	4
Leiostomus xanthurus	—	—	—	—	—	—	—	85	—	1	—	—	1	90	10	101
Menticirrhus americanus	—	—	—	—	—	—	—	—	—	—	—	—	2	2	3	7
M. saxatilis	—	—	—	—	—	—	—	—	—	—	—	3	9	10	17	36
Micropogon undulatus	—	—	—	—	—	—	—	—	8	—	—	—	—	—	8	8
Mullus auratus	—	—	—	—	—	1	—	—	1	—	—	1	—	—	3	3
Chaetodipterus faber	—	1	—	4	—	—	—	—	—	2	2	9	10	4	9	23
Chromis enchrysurus	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Halichoeres bivittatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. caudalis	—	—	—	—	—	—	—	—	3	—	—	1	—	—	4	4
Hemipteronotus novacula	2	11	—	—	10	42	—	—	1	—	—	4	9	40	55	104
Astroscopus y-graecum	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1
Trichurus lepturus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Euthynnus alletteratus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1

Table 5.—Continued.

Species	1971	Jan.-Feb.			March			April			May			June		
		T	F	A	T	F	A	T	F	A	T	F	A	T	F	A
Peprilus alepidotus		—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
P. triacanthus		3	20	—	—	—	—	—	5	3	—	—	—	—	—	—
Scorpaena brasiliensis	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. calcarata	6	6	—	—	1	14	4	2	1	1	—	1	—	—	1	1
Bellator militaris	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prionotus evolans		—	2	3	8	29	2	1	1	8	—	3	2	—	6	—
P. ophryas		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. roseus	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. scitulus		—	7	1	3	19	9	—	6	8	—	76	15	2	—	—
P. salmonicolor		—	—	1	—	1	1	—	—	7	—	—	25	—	—	—
P. tribulus		—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
Ancylopsetta quadrocellata		—	—	5	—	10	2	4	1	—	6	1	—	14	1	—
Bothus sp.		—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Citharichthys macrops		—	—	2	—	2	—	—	—	6	—	—	3	6	—	—
Cyclopsetta fimbriata	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Etropus microstomus		—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
E. rimosus		—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Paralichthys albigutta		—	11	—	8	11	9	9	—	1	1	—	—	—	—	—
P. dentatus		—	21	—	20	39	32	48	6	—	22	—	2	36	2	—
P. lethostigma		—	—	9	28	4	4	—	—	1	—	—	—	—	—	—
P. squamilentus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scophthalmus aquosus		—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Syacium papillosum	3	3	—	—	—	7	1	—	3	—	4	—	1	10	—	—
Gymnachirus melas	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trinectes maculatus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Alutera schoepfi		—	—	—	3	8	—	—	—	—	—	—	—	—	—	—
A. scriptus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Balistes capriscus	1	1	—	—	1	3	1	4	—	—	6	4	—	30	36	—
Monacanthus hispidus		—	—	1	2	7	—	1	—	—	5	—	1	28	7	—
Lactophrys quadricornis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Sphoeroides dorsalis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. maculatus		—	18	50	6	145	19	—	5	7	—	1	2	—	—	—
S. spengleri		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chilomycterus antillarum		—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
C. schoepfi		—	—	—	—	4	1	1	—	—	—	1	—	—	—	—
Subtotal		20	120	281	149	534	312	135	105	478	115	215	81	178	129	2
Total	69		421			995			718			411			309	

studies. Of those tagged, *Paralichthys dentatus* (184 specimens), *Monacanthus hispidus* (107), *Raja eglanteria* (92), *Stenotomus aculeatus* (77), *Balistes capriscus* (66), *Centropristes striata* (57), *Mustelus canis* (41), *Ancylopsetta quadrocellata* (40), *Aluterus scriptus* (35), and *Paralichthys lethostigma* (35) accounted for 74.3%. Of the 985 fishes tagged, 17 (1.7%) were recaptured involving 11 species: *Centropristes striata, Balistes capriscus, Aluterus schoepfi, Centropristes ocyurus, Calamus bajonado, Monacanthus hispidus, Paralichthys albigutta, P. dentatus, Rhinoptera bonasus, Raja eglanteria,* and *Stenotomus aculeatus. Paralichthys dentatus* and *Balistes capriscus* accounted for 6 and 2 of the recaptures respectively, while all others were single recaptures. Most recaptures were returned from near their release point on the bed. The longest period at liberty was 8 days. This, in the light of the intense fishing of the 13 boats that composed the 1972 fleet and the few recaptures, suggested that the fish population over the scallop bed was large, constantly moving, and subject to constant recruitment from elsewhere.

Stomach analysis of 1,655 of the 33 most frequently encountered fishes (Table 6) revealed that the stomachs of most of the fishes over the bed usually contained food even though all samples were made only during daylight hours; 89.4% had scallops or other food as part of the stomach contents. *Sphoeroides maculatus, Stenotomus aculeatus, Diplectrum formosum, Orthopristes chrysopterus, Monacanthus hispidus, Balistes capriscus, Centropristes striata, Mustelus canis,* and *Synodus foetens* (in descending order of species whose stomachs contained scallops) were found to be scallop predators (Table 6). Small as well as large individuals of these species had parts or whole scallops in their stomachs and digestive tracts (Table 6). These species fed either by cracking the scallop shell with their beaklike jaws (*Balistes, Sphoeroides*) or by finding dying or cracked (possibly a result of the fishing activity) individuals (*Stenotomus, Diplectrum, Orthopristes*). It was surprising that bottom feeders of the families Bothidae (*Paralichthys albigutta, P. lethostigma*), Soleidae (*Trinectes maculatus*), Rajidae (*Raja eglanteria*), Labridae (*Hemip-*

Species	July			August			September			October			1972 total			Total 1972
	T	F	A	T	F	A	T	F	A	T	F	A	T	F	A	
Peprilus alepidotus	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3
P. triacanthus	—	—	—	—	—	—	—	—	—	—	—	—	3	25	3	31
Scorpaena brasiliensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. calcarata	1	3	—	—	3	—	—	1	1	—	—	1	10	24	8	42
Bellator militaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prionotus evolans	3	7	—	3	12	5	—	7	1	1	8	4	16	75	25	116
P. ophryas	—	—	—	—	—	1	—	—	3	—	—	—	—	—	4	4
P. roseus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. scitulus	—	16	—	—	19	1	—	2	5	—	—	7	5	145	46	196
P. salmonicolor	—	—	—	—	—	8	—	—	3	—	—	—	—	1	45	46
P. tribulus	—	—	—	—	—	—	—	—	1	—	—	—	—	—	4	4
Ancylopsetta quadrocellata	9	2	—	6	3	1	1	1	4	—	—	—	40	19	12	71
Bothus sp.	—	—	—	—	—	1	—	—	1	—	—	1	—	—	4	4
Citharichthys macrops	—	—	—	—	1	10	—	—	4	—	—	—	6	3	25	34
Cyclopsetta fimbriata	—	—	—	—	—	—	—	—	1	—	—	1	1	—	2	3
Etropus microstomus	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
E. rimosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Paralichthys albigutta	—	—	—	10	3	1	3	—	5	2	—	3	33	25	19	77
P. dentatus	24	4	—	17	1	—	11	2	1	6	6	3	184	81	38	303
P. lethostigma	—	—	—	1	—	—	5	—	—	1	—	3	35	4	17	56
P. squamilentus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Scophthalmus aquosus	1	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3
Syacium papillosum	1	1	—	1	4	33	—	—	3	—	—	1	19	15	39	73
Gymnachirus melas	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1
Trinectes maculatus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Alutera schoepfi	3	—	—	12	26	2	6	14	—	3	8	—	27	56	2	85
A. scriptus	35	11	—	—	1	1	—	—	—	—	—	—	35	12	1	48
Balistes capriscus	8	4	—	10	5	—	6	1	—	—	—	—	66	53	1	120
Monacanthus hispidus	34	13	—	28	32	5	7	—	1	2	—	—	107	59	8	174
Lactophrys quadricornis	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	2
Sphoeroides dorsalis	—	—	2	—	—	1	—	—	—	—	—	2	—	—	5	5
S. maculatus	—	1	—	—	18	1	—	6	8	—	4	—	6	198	87	291
S. spengleri	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
Chilomycterus antillarum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
C. schoepfi	—	—	—	—	1	—	—	1	—	—	—	3	1	7	4	12
Subtotal	136	108	17	137	223	219	51	169	161	64	52	201	985	1,655	1,752	
Total		261			579			381			317			4,392		4,392
														Grand total		4,461

teronotus novacula), and other Balistidae (*Aluterus schoepfi*) were not active scallop predators.

Our observations agree with Roe et al. (1971), who noted that *Sphoeroides* is an active predator of calico scallops. While *Dasyatis centroura* is a possible predator (Struhsaker 1969) neither it, the dasyatids *D. americana* and *Gymnura micrura*, nor the myliobatid, *Rhinoptera bonasus*, fed on scallops.

MACROINVERTEBRATE ASSOCIATES AND PREDATORS

Field observations yielded 60 species of macromolluscs, 25 crustaceans, 12 echinoderms, 4 coelenterates, and 1 annelid as associates of the bed (Table 7). These species, their numbers, and abundances varied by season throughout the bed. Species found in 50 or more percent of the samples which may be considered the macroinvertebrates common to the beds were: *Eucrassatella speciosa, Arcinella cornuta, Cassis madagascariensis, Pleuroploca gigantea, Octopus vulgaris, Loligo pealei, Calappa falmmea, Hepatus epheliticus, Astropecten articulatus, Luidia alternata, L. clathrata, Hemipholis elongata, Toxopneustes variegatus,* and *Encope emarginata.*

Luidia clathrata and *Astropecten articulatus* occurred abundantly throughout the bed during all seasons and were predators of scallops (Table 7). The following were found less abundantly and were suspected predators of calico scallops: *Asterias forbesii, Busycon carica, B. contrarium, B. spiratum, Fasciolaria hunteria, F. tulipa, Loligo pealei, Murex fulvescens, M. pomum, Octopus vulgaris, Pleuroploca gigantea, Polinices duplicatus, Strombus alatus, Arenaeus cribrarius, Calappa flammea, Hepatus epheliticus, Libinia emarginata, Ovalipes quadulpensis,* and *Portunus spinimanus.*

The most common sea stars on the 1972 calico scallop grounds were *Astropecten articulatus, Luidia alternata,* and *L. clathrata. Goniaster americanus, Echinaster brasiliensis, Asterias forbesi,* and *Gorgonocephalus arcticus* were noted in lesser numbers (Table 7). Identifications were

TABLE 6.—Analysis of 1,655 stomach contents from 46 species of fishes captured on the scallop grounds during commercial operations between February and October 1972.

Species	Cruises occurred in	Specimens examined	Size range	Number eating		
				Scallops	Other food	Empty
Carcharhinus obscurus	2	1	960		1	
Mustelus canis	8	33	440-972	13	15	5
Squatina dumerili	2	1	1,160		1	
Raja eglanteria	20	135	136-580	7	127	1
Dasyatis americana	4	1	676		1	
Gymnura micrura	4	1	415		1	
Gymnothorax nigromarginatus saxicola	2	1	276		1	
Synodus foetens	23	200	98-426	11	163	26
Trachinocephalus myops	6	8	170-216	1	2	5
Opsanus tau	2	1	246		1	
Porichthys porosissimus	6	8	146-210		8	
Lophius americanus	4	3	560-716	1	1	1
Urophycis regius	2	4	110-208	1	1	2
Centropristis ocyurus	4	7	112-172	6	1	
C. striata	15	57	92-325	21	28	8
Diplectrum formosum	9	67	46-282	37	23	7
Pomatomus saltatrix	3	1	138		1	
Haemulon plumieri	6	1	230		1	
Orthopristis chrysopterus	14	47	116-216	36	6	5
Calamus senta	6	15	120-225		15	
Lagodon rhomboides	4	10	87-122		10	
Stenotomus aculeatus	22	101	90-256	64	27	10
Leiostomus xanthurus	4	90	144-188	1	86	3
Menticirrhus americanus	2	2	170-262		2	
M. saxatilis	5	10	190-280	1	8	1
Chaetodipterus faber	9	4	286-290		4	
Hemipteronotus novăcula	17	40	128-172	7	26	7
Peprilus alepidotus	2	3	118-156		3	
P. triacanthus	2	25	97-156	1	4	20
Scorpaena calcarata	15	24	64-142	1	23	
Prionotus evolans	19	75	196-342	2	61	12
P. salmonicolor	6	1	186-222		1	
P. scitulus	19	145	134-268	2	136	7
Ancylopsetta quadrocellata	28	19	170-290		19	
Citharichthys macrops	11	3	120-142		3	
Etropus microstomus	3	1	158		1	
Paralichthys albigutta	21	25	200-289		25	
P. dentatus	42	81	153-370		81	
P. lethostigma	14	4	210-500		4	
Syacium papillosum	8	15	86-300	1	13	1
Aluterus schoepfi	14	56	342-390		56	
A. scriptus	3	12	90-222	1	5	6
Balistes capriscus	18	53	105-356	20	28	5
Monacanthus hispidus	14	59	92-222	23	20	16
Sphoeroides maculatus	21	198	68-268	77	94	26
Chilomycterus schoepfi	6	7	72-142	2	4	1
Total, number				337	1,143	175
percent				20.4	69.0	10.6

based upon Gray et al. (1968) and Downey (pers. commun.).

Roe et al. (1971) suggested that *Asterias forbesi* may be a major predator on the calico scallops of the Cape Canaveral grounds. The low total percent of its occurrence on the 1972 North Carolina calico scallop grounds (Table 7) precludes this assumption for the 1972 fishery. Stomachs of *A. forbesi* were not examined because it everts its stomach when feeding (Hyman 1955:369). Hyman (1955) made no mention of the feeding habits of sea stars belonging to the Goniasteridae, Echinasteridae, or the Gorgonocephalidae. Stomachs of species belonging to these families (*Goniaster americanus*, *Echinaster brasiliensis*, and *Gorgonocephalus arcticus*) contained no recognizable material. What they were feeding upon is not known but, in light of their small numbers on the scallop beds and the lack of scallops in their stomachs, it is assumed that they were not significant scallop predators on the 1972 bed.

Luidia alternata frequented the calico scallop bed yet was not as common as either *L. clathrata* or *Astropecten articulatus* (Table 7). Stomach contents yielded no calico scallops. Several specimens were found in the field feeding upon smaller *A. articulatus*. One large living specimen, held in an experimental tank under controlled environmental conditions with living calico scallops, showed no interest in the scallops but was seen feeding upon *A. articulatus* and *L. clathrata*. It did attempt unsuccessfully to feed on a *Asterias forbesi*

TABLE 7.—Macroinvertebrate fauna of offshore calico scallop beds in 1972 by season and areas of good and poor catches. N = number of samples, data listed as percent of N.

Taxa	Mar.-Apr. N = 14	May-June N = 10	July-Aug. N = 14	Sept.-Oct. N = 10	Total N = 48	Good scallop catches N = 40	Poor scallop catches N = 8
COELENTERA							
Renillidae:							
Renilla reniformis	7				2	2	
Actiniaria (sea anemones)	14	20			8	10	
Madreporaria (corals)				20	4	5	
ANNELIDA							
Aphroditidae:							
Aphrodita hastata	7				2	2	
MOLLUSCA							
Arcidae:							
Arca imbricata			7		2	2	
A. zebra	14	10	7	10	10	12	
Anadara floridana	36	20	21		21	25	
Noetia ponderosa			14		4	5	
Mytilidae:							
Brachidontes modiolus	14	30	36		21	25	
Pteriidae:							
Pteria colymbus	14			10	6	15	
Pectinidae:							
Aequipecten muscosus				10	2	2	
Argopecten gibbus	93	100	71	80	85	100	13
Lyropecten nodosus		10	21	10	10	10	13
Pecten reveneli	21	30	21	30	25	28	13
Ostreidae:							
Ostrea permollis			7	20	6	7	
Chamidae:							
Arcinella cornuta	43	40	79	30	50	55	25
Chama macerophylla		10			2	2	
Crassatellidae:							
Eucrassatella speciosa	43	40	86	10	48	50	38
Cardiidae:							
Dinocardium robustum	7	10	14	20	13	13	13
Laevicardium multilineatum	21	10	21	10	17	15	25
Veneridae:							
Chione intapurpurea	7	10	43	30	23	18	50
C. latilirata	29	20	64	40	40	35	63
Macrocallista maculata	57	20	43	20	38	43	13
M. nimbosa		10			2	2	
Solenidae:							
Ensis directus				10	2	2	
Tellinidae:							
Tellina magna			7		2		13
T. nitens				10	2	2	
Solecurtidae:							
Solecurtus cumingianus	7				2	2	
Trochidae:							
Calliostoma euglyptum			7	10	4		25
Turbinidae:							
Astraea phoebia			7		2		13
Turbo castanea		10	14	30	13	15	13
Architectonicidae:							
Architectonica nobilis		10		10	4	5	
Cerithiidae:							
Cerithium litteratum							
Xenophoridae:							
Xenophora conchyliophora	14	30	7	20	17	20	
Strombidae:							
Strombus alatus	14	50	57	30	38	45	
S. costatus			7		4	2	
Cypraeidae:							
Cypraea cervus			14		4	5	
Naticidae:							
Natica canrena			7	10	4	5	
Polinices duplicatus	36	20	50	20	33	35	25
P. duplicatus eggs	7				2	2	
Sinum maculatum	7	10	7	20	10	12	
Cassididae:							
Cassis madagascariensis	21	80	79	50	56	60	38
C. madagascariensis eggs		20			4	5	
Cypraecassis testiculus			7		2	2	
Phalium granulatum	21	20	36	20	25	25	25
P. granulatum eggs		10			2	2	
Cymatidae:							
Distorsio clathrata	7	20	21		13	15	
Tonnidae:							
Oocorys abyssorum							
Tonna galea	7	40	7		13	15	

Table 7.—Continued.

Taxa	Mar.-Apr. $N = 14$	May-June $N = 10$	July-Aug. $N = 14$	Sept.-Oct. $N = 10$	Total $N = 48$	Good scallop catches $N = 40$	Poor scallop catches $N = 8$
Ficidae:							
Ficus communis	7	20	14		10	12	
Muricidae:							
Eupleura caudata			7		2	2	
Murex dilectus			7		2		13
M. fulvescens	29	30	71		35	40	13
M. fulvescens eggs			14		4	5	
Murex pomum	21	30	29	40	29	28	38
Thais haemastoma floridana				10	2	2	
Melongenidae:							
Busycon canaliculatum			7		2	2	
B. carica		20	7	20	10	10	13
B. contrarium	29	10		20	15	15	13
B. contrarium eggs	21				6	7	
B. spiratum	21	20	14	30	21	23	13
B. spiratum eggs	14				4	5	
Fasciolariidae:							
Fasciolaria lilium hunteria	7	40	57	20	31	30	38
F. l. hunteria eggs			14		4	5	
F. tulipa	21	30	21	10	21	23	13
F. tulipa eggs	7				27	2	
Pleuroploca gigantea	43	70	50	70	56	55	63
P. gigantea eggs		10	7	4	5		
Olividae:							
Oliva sayana Ravenel	43	10	50	20	33	35	25
Cancellariidae:							
Cancellaria reticulata	7						
Conidae:							
Conus delessertii	7	30	14		13	15	
Octopodidae:							
Octopus vulgaris	71	70	93	60	75	75	75
Loliginidae:							
Lolliguncula brevis	7				2	2	
Loligo pealeii	71	50	93	60	71	70	75
ARTHROPODA							
Stomatopoda:							
Gonodactylus aerstedi	21	20	14		15	17	
Penaeidae:							
Penaeus sp.	29	20	7	20	19	22	
Sicyonia brevirostris	21	10	29	30	23	21	13
Scyllaridae:							
Scyllarides nodifer	7	20		10	8	10	
Porcellaridae:							
Porcellana sayana	14				4	5	
Paguridae:							
Pagurus sp.	7			10	4	5	
P. annulipes		60	64	40	40	40	38
P. pollicaris		40	64	40	35	35	38
Raninidae:							
Ranilia muricata	14		7		6	7	
Calappidae:							
Calappa angusta	7			10	4	5	
C. flammea	64	60	79	60	67	73	38
Hepatus epheliticus	43	70	64	70	60	65	38
Osachila sp.				10	2		13
Portunidae:							
Ovalipes quadulpensis	21				6	7	
O. ocellatus	21	30	36	10	25	25	25
Portunus gibbesii	57	40	36	30	42	45	25
P. spinimanus	7			30	8	10	
Callinectes sapidus							
Arenaeus cribrarius	7	10			4	5	
Cancridae:							
Cancer irroratus	7				2	2	
Majidae:							
Libinia emerginata	36	50	36	40	40	43	25
Stenocionops furcata coelata				10	2	2	
Parthenopidae:							
Parthenope serrata	14				4	5	
P. pourtelesii				10	2	2	
Xiphosura:							
Xiphosura polyphemus	43	50	50	10	40	40	38
ECHINODERMA							
Astropectinidae:							
Astropecten articulatus	100	90	93	80	92	93	88
Luididae:							
Luidia alternata	57	90	86	20	65	70	38
L. clathrata	100	100	93	90	96	98	88

Table 7.—Continued.

Taxa	Mar.-Apr. $N = 14$	May-June $N = 10$	July-Aug. $N = 14$	Sept.-Oct. $N = 10$	Total $N = 48$	Good scallop catches $N = 40$	Poor scallop catches $N = 8$
Goniasteridae:							
Goniaster americanus	7	40	7		13	13	13
Echinasteridae:							
Echinaster brasiliensis	14	30	14	30	21	23	13
Asteriidae:							
Asterias forbesi	7	30			8	10	
Gorgonocephalidae:							
Gorgonocephalus arcticus		10		10	4	3	13
Amphiuridae:							
Hemipholis elongata	79	70	64	60	69	73	50
Arbaciidae:							
Arbacia punctulata	7	60	64	60	46	45	50
Toxopneustidae:							
Toxopneustes variegatus	36	80	79	60	63	65	50
Scutellidae:							
Encope emarginata	64	50	71	30	56	60	38
Cucumariidae:							
Thyone briareus	29			10	10	12	

and was noted to have killed a large *Strombus alatus*. Hyman (1955:369) pointed out that species of *Luidia* eat mainly other echinoderms. At this time, we do not consider *L. alternata* a calico scallop predator.

Luidia clathrata was a predator of calico scallops (Table 8). Between March and June we found small numbers of scallop valves (ranging from 0.9 to 11.6 and 21.1 to 45.3 mm) in *L. clathrata* stomachs (Table 9). Maximum predation took place (April) just as calico scallop spawning began. Why large scallops (21-45 mm lengths) were fed on only in March and April is not known. The data does indicate that numbers of *Luidia* (Table 10) large enough (110 to 160 mm?) to swallow the available scallops (28 to 70 mm length) were more available during March through June. Preliminary observations on *L. clathrata* kept in the laboratory indicated that they will feed readily on calico scallops, digestion occurring within 24 h. Hulings and Hemlay (1963) found *L. clathrata* to engulf sediments and utilize whatever was available as food.

Wells et al. (1961) suggested that *A. articulatus* was a nonselective feeder, while Porter (1972b)

TABLE 9.—Average number of calico scallop valves found per month in stomach samples of sea stars *Astropecten articulatus* and *Luidia clathrata* sampled in 1972 on the producing calico scallop beds off North Carolina.

Month	*Astropecten articulatus*		*Luidia clathrata*	
	No./100 stomachs[1]	No. stomachs examined	No./100 stomachs[1]	No. stomachs examined
Feb.	1	85	0	71
Mar.	7	226	6	87
Apr.	7	151	28	178
May	158	67	17	66
June	29	314	7	311
July	8	86	3	36
Aug.	2	154	0	56
Sept.	7	89	0	43
Oct.	3	67	0	20

[1]Approximate number.

TABLE 10.—Monthly lengths (millimeters) for sea stars captured on the calico scallop beds in 1972.

Month	*Astropecten articulatus*			*Luidia clathrata*		
	Average arm length	Size range	Sample size	Average arm length	Size range	Sample size
Feb.	61.6	34-101	109	92.7	46-142	72
Mar.	63.3	24-111	433	95.6	58-155	134
Apr.	60.0	18-124	176	91.2	27-166	227
May	58.9	35-122	125	88.2	40-140	110
June	61.1	25-134	497	88.8	50-160	315
July	64.8	28-103	112	89.6	61-122	42
Aug.	64.5	28-120	169	84.6	28-112	85
Sept.	83.1	35-136	113	87.0	51-134	44
Oct.	62.2	23-124	101	89.6	23-124	22

TABLE 8.—Lengths (millimeters) of calico scallop valves removed from stomachs of sea stars *Astropecten articulatus* and *Luidia clathrata* collected on the calico scallop beds during the 1972 catch season.

Sea star	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Astropecten articulatus:									
Average valve length	1.8	2.4	1.9	2.3	3.0	2.9	2.3	2.9	4.5
Size range	1.8	1.6-3.8	0.7-4.3	0.9-3.6	0.7-6.4	2.3-3.6	1.4-2.6	1.7-2.6	3.3-5.6
Number valves found	1	8	10	62	39	5	4	5	2
Luidia clathrata:									
Average valve length	—	4.3	1.9	2.4	3.3	4.2	—	—	—
		33.9	43.7		21.1				
Size range	—	2.4-11.6	0.9-6.9	1.4-3.5	1.0-6.4	4.2-4.2	—	—	—
		30.0-40.4	41.0-45.3		21.1				
Number valves found	—	5	39	9	14	1	—	—	—
		5	5		1				

showed that large numbers of recently set calico scallops may be eaten by *A. articulatus* and that though continued examination of their stomach contents, knowledge may be gained concerning when and where calico scallop setting takes place. During May and June 1972, numerous small scallop valves appeared in the stomachs of this sea star (Table 10). Valve numbers/100 stomachs were not nearly as many as the 3,000/100 stomachs reported by Porter (1972a) for June 1971. It is inferred from this that the 1972 scallop set on the sampled grounds was relatively small. Note that numbers of dead scallop shells increased from July through October when the fishery collapsed (Table 11). Also, the presence of *L. clathrata* decreased while *A. articulatus* presence increased during the March to October period (Table 11).

Stomach content data (Table 10) suggested that if there were scallop spawnings following the initial May spawning as we have theorized, then the set from these and the May spawnings either did not survive after June or the setting occurred in an area not covered by the sampling. Stomach analysis data of sea stars continues to be worked up and evaluated.

TABLE 11.—Average monthly numbers of dead shells and sea stars per bushel catch (N) occurring on the calico scallop beds in 1972.

Month	N	Dead shells	*Luidia clathrata*	*Astropecten articulatus*
Mar.	13	23	8	5
Apr.	8	19	5	4
May	2	19	1	2
June	8	22	1	2
July	7	106	2	6
Aug.	11	220	3	3
Sept.	4	134	1	8
Oct.	1	290	2	55

DISCUSSION

We had expected to find that the calico scallop bed(s) that sustained the 1972 North Carolina fishery to have been distinct in either physical, chemical, or biological features. Instead, few differences were found which could be pinpointed as factors that made the bed(s) more unique than the surrounding shelf areas. We noted that bottom texture within and without the beds studied were nearly identical (Table 3). Likewise, no extremes of water temperatures, salinities, or phytoplankton population (as measured by chlorophyll a levels) seemed to exist in 1972. While the fish and invertebrate faunas were diverse and speciose, they too were little different from that noted from the nearby reefs or areas (Pearse and Williams 1951; Wells et al. 1964; Cerame-Vivas and Gray 1966). Seasonal shifts in the fishes and invertebrates inhabiting the bed(s) occurred but these were directly related to seasonal water temperatures, salinities, or their natural migrating movements (Tables 5, 7). Most populations of fishes apparently moved over the bed(s) constantly, some 24 species (of 33 most abundant) feed on scallops. Of the macroinvertebrates, 3 species of sea stars and 19 other macroinvertebrates were predators. Whether the fishes and sea stars or other macroinvertebrate predators, which were definite predators of calico scallops, were attracted to the area because of the scallops or the activities of the fishery, which created available food in the form of broken scallops, remains unresolved. One interesting correlation was noted in that the painted wrasse, *Halichoeres caudalis,* appeared over the bed, in September and October, as increased numbers of dead scallops occurred just prior to the demise of the 1972 fishery on 28 October. This relationship has also been noted for the Cape Canaveral calico scallop beds of Florida (George Miller pers. commun.).

While we document the fish and macroinvertebrate faunas and the ecology of a North Carolina bed(s) that sustained the 1972 fishery, we are still at a loss as to what creates the vacillations of scallop availability in a bed or why one bed prevails over another during any one or succeeding years. Note that while the experimental bed was fished and did possess scallops throughout 1972, it as well as the commercial bed failed to support scallops in the years 1973 through 1976. We cannot ultimately conclude that the 1972 bed and fishery collapsed as a sole result of overfishing but that the levels of scallops available after 28 October could not economically support the fleet. Sampling the planktonic stages of calico scallops may resolve the repopulation aspects of the beds for we still do not know whether we are simply at the northern edge of its range, which may be dependent on larval drift and recruitment from more southern areas, or are dealing with a population dependent upon native larvae for repopulation. Additional field observations of the shelf water mass movements and how they affect the survival, growth, and existance of scallops needs refinement while laboratory experiments which vary a number of ecological parameters will hopefully

resolve what permits a calico scallop bed to exist.

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In galley: we anticipate Rick Dawson's revision of *Stenotomus* and list our *S. caprinus* as *S. aculeatus*.

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NOTES

ENERGY FOR MIGRATION IN ALBACORE, *THUNNUS ALALUNGA*

The relations between immigrants and residents of a specific fishing ground can likely be evaluated from examination of the relative fat content of individuals from a time sequenced sampling of the fishery. These kinds of information are not yet estimable for pelagic populations.

The problem of energy availability and utilization in migrations of fish is a perplexing one. Migrations are energetically quite expensive unless a fish is passively carried by currents. Recently recorded migrations of two tagged albacore, *Thunnus alalunga* (Bonnaterre), across the Pacific Ocean indicate that they traveled an average of 48 km/day (Japanese Fisheries Agency 1975). As these fish were approximately 80 cm long on release, the average migration speed was about 0.65 body lengths/s (55.6 cm/s). This is well within the range of observed swimming speeds for this species. These albacore were reported to have traveled from lat. 35°41′N, long. 171°37′E (Figure 1, point E) to lat. 47°00′N, long. 125°30′W (Figure 1, point F), a distance of 5,239 km in 110 days. The caloric equivalent, in grams of fat,[1] utilized by these two fish at the estimated rate of travel of about 55 cm/s would be about 1,450 g or 14.5% of their expected weight at the onset of migration. Although great amounts of feed would not be necessary for this migration given the 1 kcal/g average available caloric content for forage (Sharp and Francis 1976), the albacore has been reported to have up to 18.2% fat in the edible flesh portions (Sidwell et al. 1974). Muscle tissue constitutes 58.2% of the total body weight of albacore (Dotson unpubl. data) which means up to 10.6% body weight in fat has been observed, a value approaching that necessary to provide the caloric energy for these migrations.

There is little doubt that albacore do not migrate directly, that feeding does occur, and that the fish probably do grow in overall length and

[1]9.4 kcal/g fat.

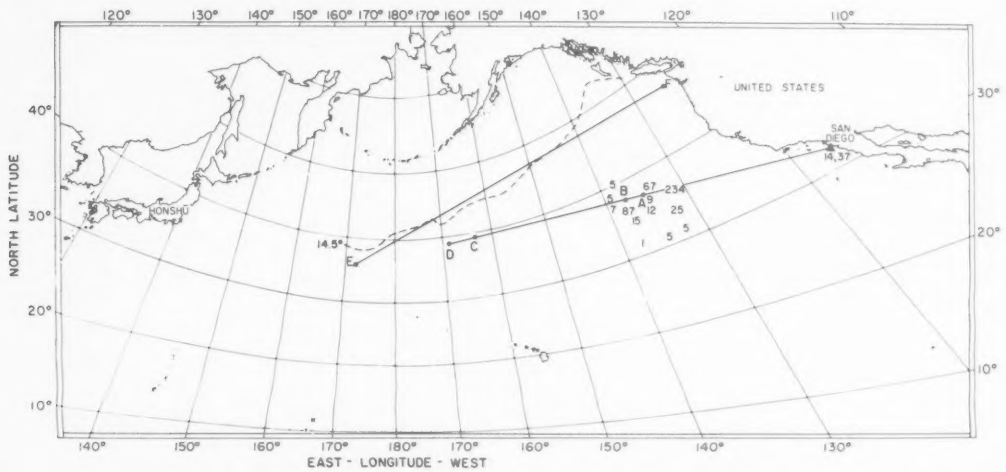

FIGURE 1.—A great circle plotting chart is shown and the quantity and location of albacore samples is indicated by the numerals. A length-mass equation was developed for the 477 albacore caught west of long. 130°W during June 1974. The numbers 14 and 37 near San Diego represent the samples collected in July and September 1975, respectively. Using ▲ as the origin the letters A and B along the line represent the distances which a 63-cm albacore could swim utilizing 404 g of fat at A, its minimum speed; B, the observed diurnal-nocturnal activity level. Points C and D on the same line represent the distance that the 65-cm fish with the greatest observed mass deficit (999 g) could have traveled utilizing the energy of this quantity of fat at the two respective activity levels described above. Points E and F are the release and recapture positions of two albacore tagged by Japanese researchers. The minimum temperature habitat limit of albacore (14.5°C) is depicted by a dashed line. The great circle route does not differ markedly from this boundary but likely represents a conservative estimate of the total distance traveled between points E and F.

mass during the migratory period. What appears to be an important question is whether or not the migrations of albacore and other tunas are extra demanding, meaning sufficient short-term energy is required to induce fat store utilization even though feeding is still accomplished. Too often the concepts of growth and fat deposition are integrated such that it is considered unlikely that morphological growth can take place during fat store utilization. Certainly from observations of adolescent growth in mammals it is obvious that there is no necessary dichotomy here. The two processes require separate biochemical pathways and are very likely separated temporally, well within the standard day.

In a preliminary effort to examine the question of fat utilization, the length-mass relationship of albacore collected offshore preceding their appearance in the onshore eastern Pacific surface fishery has been compared with fish freshly arrived in this fishery, and with fish which have presumably been grazing and reconditioning for the postsummer exodus from the onshore area. Calculations from these data support the hypothesis that fat stores are utilized for migration energy.

We hope that these calculations and subsequent inferences will stimulate further research into the considerable problem of highly variable length-mass information and its potential use in studies of migratory fishes.

Observations

In June 1974, 477 albacore 463 to 794 mm long were captured in the area between long. 130° to 140°W and lat. 30° to 40°N (Figure 1). A curve was fitted by regression to the length-mass data from these fish resulting in the equation (Dotson 1977),

$$M = 4.514 \times 10^{-5} L^{2.8746} \quad (1)$$

where M is the mass in grams and L the fork length in millimeters. Measured values fell within 250 g of the regression line.

Mass and length measurements were made on 14 albacore (600 to 657 mm FL, mean 631) collected during July and 37 fish (516 to 851 mm FL) collected during September 1975, in a region 110 km south of San Diego, Calif. (Figure 1). The mass of September-caught albacore was not different from those estimated by the length-mass regression curve. The mass of July-caught albacore, however, averaged 404 g below those estimated by regression (range: 172 g greater to 999 g less). Analysis of body densities indicated that the mass deficit of the albacore caught in July was probably due to fat loss, or simply stated, as a fish of a given length gets lighter its density increases (Dotson 1977).

The albacore fishery near the coast commenced in July 1975. The albacore in this fishery are known to migrate from the offshore region (Laurs and Lynn in press), and it is assumed, therefore, that the mass (fat) deficit was utilized as an energy source during migration to the coast.

Calculations and Inferences

Using the observed mass deficits observed in the July 1975 sample, it is possible to estimate the migration path length assuming 1) little or no growth occurs during the migration, and 2) the fat utilized is the only energy source during migration.

Based upon studies of swimming energetics of tunas, Sharp and Francis (1976) estimated the relation between swimming speed (V) in centimeters per second, fork length (l) in centimeters, and the swimming caloric expenditure per unit time (C_s) in kilocalories per hour. The basic equation for this relation, in calories utilized per hour, is as follows:

$$C_s = 8.7 \times 10^{-8} (l)^2 (V)^3 Cd. \quad (2)$$

The coefficient of drag (Cd) is estimated using the relation (Sharp and Francis 1976)

$$Cd = 0.262 \exp [-(4.805 \times 10^{-6}) Re] \quad (3)$$

where Re (Reynolds number) $= lV/\nu$ (at $Re \geq 6.8 \times 10^5$, $Cd = 0.01$), ν is the kinematic viscosity of seawater, approximated by the value 0.01.

Sharp and Francis (1976) also estimated the metabolic maintenance energy (C_m) (i.e. stasis energy requirements) for tunas to be 1 g cal/g per h. The metabolic weight (W_{met}) is approximated by the relation

$$W_{met} = (M_f)^{0.8} \quad (4)$$

$$C_m = W_{met} \times 10^{-3} \text{ kcal/g per h} \quad (5)$$

where M_f is the mass of the fish in grams.

Assuming that the mean mass deficit of 404 g of

the albacore caught in July was fat loss and given that fat yields about 9.4 kcal/g, less ~15% due to the cost of fat mobilization (SDA), leaving about 8.0 kcal/g, the caloric value of the fat loss is 3,272 kcal. The mean length of the albacore in the July sample was 63 cm with a computed mass for the offshore region (from Equation (1)) of 5,030 g. As this would be the weight at the initial stage, it seems appropriate to use as the mass for the calculations the equivalent of one-half of the observed loss in mass (202 g) subtracted from the computed initial mass to give a value of 4,828 g. Using these equations, the rate of caloric expenditure per hour was estimated for a 63-cm albacore swimming at 54 cm/s which is the estimated minimum speed a 63-cm albacore can swim and maintain hydrostatic equilibrium, V_{100} (Magnuson 1970; Dotson 1977). Where C_s plus C_m is equal to the total caloric expenditure (C_{total}) during migration, then:

$$\begin{aligned} C_{\text{total}} &= C_s + C_m \\ &= 2.78 \text{ kcal/h} + 0.89 \text{ kcal/h} \\ &= 3.67 \text{ kcal/h}. \end{aligned} \qquad (6)$$

The caloric equivalent of the fat divided by the hourly caloric utilization rate, C_{total}, Equation (6) yields the number of hours that swimming at 54 cm/s could be sustained utilizing this energy source alone and is estimated to be

$$\frac{3{,}272 \text{ kcal}}{3.67 \text{ kcal/h}} = 892 \text{ h or } \sim 37 \text{ days}.$$

The speed and time multiplied together yield the linear distance traveled during this period. This was calculated to be 1,730 km (935 nmi).

Based upon sonic tracking experiments, the average swimming speeds of three albacore 84, 85, and 87 cm in length have been observed to be 95 cm/s during the day and 62 cm/s at night (Laurs et al. 1977). The minimum swimming speed for hydrostatic equilibrium of these fish (V_{100}) is estimated to be about 42 cm/s (Dotson 1977). Assuming the ratio of observed speed (V_0) to minimum speed (V_{100}) to be relatively constant over the size range, then diurnal and nocturnal speeds can be estimated where V_0/V_{100} = 42 cm/s = 2.260 is the multiplier for daylight speeds and (62 cm/s)/(42 cm/s) = 1.575 is the multiplier for night speeds. The result of this estimation is that the daylight and nighttime speeds for a 63-cm albacore are 122 and 80 cm/s, respectively. Assuming equal time spent at each speed, about 6.08 kcal/h are utilized. If the tracking observations are representative of migratory swimming speed, and therefore caloric expenditures, then the fat energy would have been utilized in a period of nearly 22 days and the linear distance traveled would be about 1,960 km (1,060 nmi).

From the nearshore area of capture, the maximum linear distance traveled using the average fat loss of a 63-cm albacore is indicated by points A and B in Figure 1. The two values indicated represent a) 37 days at a minimum speed of 54 cm/s, and b) the estimated diurnal rates of 80 and 122 cm/s for equal portions of 22 days. The interesting result is that both the distances are within the area where the offshore samples with the greater length-mass relationship were collected and compared with the onshore material.

The maximum observed mass difference from the offshore mean of an albacore caught inshore is 999 g or 18% of its body weight for a 65-cm fish (Dotson 1977). Assuming the total weight difference to be fat, at its calculated minimum speed of 54 cm/s, this albacore could have traveled 4,200 km (2,270 nmi) over a period of 90 days utilizing only this fat as an energy source. This would place the fish well out in the mid-Pacific, as shown by point C in Figure 1. Swimming at the estimated day and night speeds of 122 and 80 cm/s for equal parts of the day this fish could travel 4,680 km (2,520 nmi) in 54 days (Figure 1, point D).

These observations, calculations, and hypotheses should indicate some of the potential effects which can be examined in the future, given broad-scale sampling and interest in the migrations of tunas. Fat content is an important indicator of the calories available for migration and/or spawning in fish of sufficient maturity. The importance of immigrants to population assessment in managed fisheries is obvious. Certainly, spawning success and behavior is dependent upon the available caloric stores. For tunas where migration and grazing up to spawning condition may be competitive processes, a thorough examination of the fat level cycles may offer insights into both periodicity and location of the potential spawners. This is an area of minimal understanding in tunas to date. Considering the importance of these processes in the life cycles of tunas, it seems that a certain amount of importance should be placed upon obtaining comprehensive data from several behavioral categories of tunas where inferences could be made about the relation of fat stores and behavior.

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GARY D. SHARP

Inter-American Tropical Tuna Commission
La Jolla, CA 92038

RONALD C. DOTSON

Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, CA 92038

UNDERWATER SOUNDS FROM RIBBON SEAL, *PHOCA (HISTRIOPHOCA) FASCIATA*[1]

Intense downward frequency "sweeps" and broadband "puffing" sounds were recorded underwater in the presence of ribbon seal, *Phoca (Histriophoca) fasciata* Zimmerman 1783. The recordings were made in the waters off Savoonga, St. Lawrence Island, Alaska, on 16, 17, 18, and 23 May 1967.

The seals were encountered in the final ice of the spring made up of windrows of small to moderate floes mixed with brash ice, and with stretches of up to 1 km of open water between. On this ice typically occur adults and pups of a variety of other pinniped species (*Phoca largha, Erignathus barbatus, Pusa hispida,* and *Odobenus rosmarus*), but during the spring of 1967 there was a preponderance of *Histriophoca* in this area. This is reflected in the records of the pinniped harvest for this area (Alaska Department of Fish and Game) which show that *Histriophoca* usually composes less than 2% of the catch, but in 1967 it made up 60% of the harvest and most of the *Histriophoca* were caught during the last half of May. The 1967 underwater recordings showed similar differences, contrasting sharply with previous years when *Erignathus* dominated the underwater sound ambient (Ray et al. 1969).

Relatively little is known of the behavior of *Histriophoca* (cf. Scheffer 1958; King 1964). Breeding assemblages occur on ice that rarely approaches shore (Burns 1970) and other social behavior may mostly occur in the water.

Instruments and Methods

Underwater sounds were recorded with a Chesapeake Instrument Corp.[2] hydrophone system and a Nagra III B tape recorder whose combined response was 50 Hz to 18 kHz (±2 dB, decibels). The sounds were studied by means of a Kay Elemetrics 7029A spectrographic analyzer and time sequences were measured by a Tektronix 565 oscilloscope.

To make the recordings, appropriate *Histriophoca* habitat in the sea ice was located with the aid of Eskimo hunters, and their skin boat was allowed to drift with the ice while the hydrophone was in the water. Only a few of these seals were seen as we approached, and they always submerged and were difficult to find again. However, some of their underwater sweep sounds were loud enough to be audible in air, implying that these seals were not far away.

Taped sequences of 5 to 8 min duration were analyzed from each of nine locations over 4 days of field study. Higher level underwater sounds, presumably from nearby seals, were analyzed and compared with background lower level sounds. Sounds from distant animals were not used for detailed analysis.

As is usually the case with underwater record-

[1]Contribution No. 3753 from the Woods Hole Oceanographic Institution.

[2]Reference to manufacturers does not imply endorsement by the National Marine Fisheries Service, NOAA.

ings, the attribution of these sounds to *Histriophoca* is circumstantial since they are underwater sounds from animals out of sight below the surface. These sounds are unlike sounds attributed to any of the other animals known to inhabit the area: gray whales (Asa-Dorian and Perkins 1967; Cummings et al. 1968; Fish et al. 1974), walrus (Schevill et al. 1966; Ray and Watkins 1975), and the ringed seal and spotted seal (Schevill et al. 1963; Stirling 1973; Ray pers. obs.). The bearded seal, *Erignathus barbatus,* was seen at times in low numbers during May 1967; some of the recordings have a background that we recognize as from *Erignathus,* but we eliminate it because: 1) the *Histriophoca* sounds are very different from the *Erignathus* sounds heard at this season (Ray et al. 1969); 2) in previous years when only *Erignathus* was nearby, none of the *Histriophoca* sounds was heard; 3) *Histriophoca* sounds were heard in the presence of these seals whether *Erignathus* were audible or not; and 4) none of these sounds were heard unless *Histriophoca* were observed in the area.

The recordings were made in a variety of ice conditions and ice is known to produce sounds underwater (Schevill 1966; Watkins and Ray pers. obs.). The seal sounds did not vary with the ice and did not match the kinds of sound we associate with ice.

Underwater Sounds

Two types of underwater sounds were heard in the presence of *Histriophoca:* a relatively intense prolonged downward sweep in frequency and a broadband puffing sound. These calls were heard sporadically, with no obvious pattern to repeated sounds nor to any answering calls. Nearby seals could be heard at least once in 2 min and often there were enough seals in audible range so that when calling was most frequent we recorded 3 to 5 calls in 10 s. Since the seals were out of sight and probably underwater during the recordings, we could not correlate the sounds with behavior.

The sweep sound (Figure 1) varied in frequency from 7 to 0.1 kHz in downward sweeps of 2 to 5 kHz each. Of the 120 sweep sounds measured, all but one could be separated into three length categories (Figure 2), each with somewhat different starting and ending fundamental frequencies:

Short sweeps,	1 s or less,	sweeping from 2000-1750 Hz to 300 Hz.
Medium sweeps,	1.3 to 1.8 s,	sweeping from 5300-2000 Hz to 100 Hz.
Long sweeps,	4 to 4.7 s,	sweeping from 7100-3500 Hz to 2000 Hz.

Short sweeps were common in the background ambient sound, but only a few were heard from nearby seals (16 measured). Midlength sweeps were the ones most often heard from local seals (84 measured), and some of these began with a short segment of sound at constant frequency for the first 0.1 to 0.2 s before beginning the downward frequency sweep (Figure 1). The long sweeps were not particularly abundant but were conspicuous

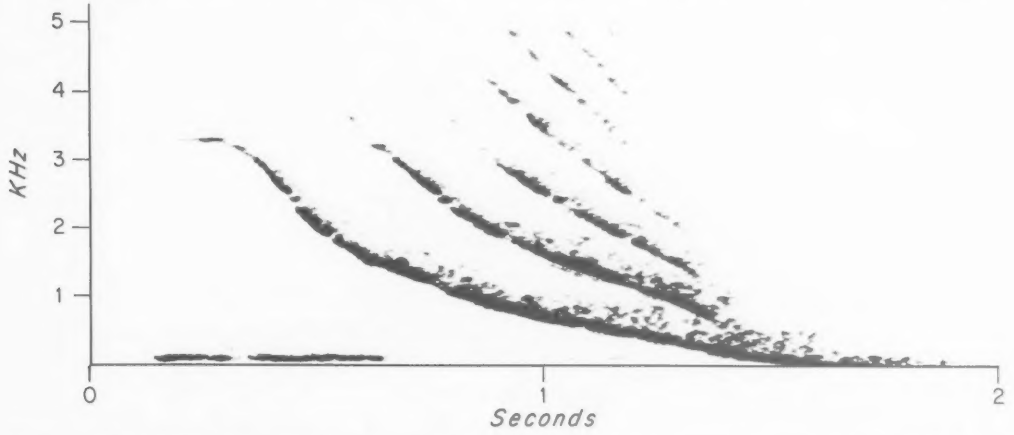

FIGURE 1.—The midlength sweep sound of *Histriophoca* often has a short portion of constant frequency before it begins to sweep downward in frequency. Analyzing filter bandwidth was 45 Hz. Analyses of short and long sweeps (not figured separately) were generally similar in character to the midlength sweep.

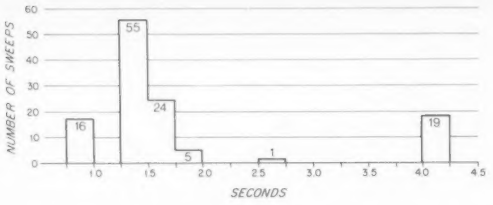

FIGURE 2.—Lengths of 120 sweep sounds from *Histriophoca* separate all but one (at 2.75 s) into three categories.

(19 measured) because of the higher frequency ending. Harmonics (up to 6 or more) were consistently present in the spectrographic analyses of even low-level sweep sounds, and appear to be a result of the pulsed character of the seal sounds (Watkins 1967).

Since we never knew the distance to calling seals, we did not have accurate acoustic source levels for these sounds. Some sweeps overloaded the recording system at the usual gain settings and therefore were received at levels estimated in excess of 40 dB (re 1 volt/dyne·cm^2). Assuming a 60-65 dB source level at 1 m and spherical spreading losses, these very loud sounds were sometimes from animals that were only 15 to 20 m from the hydrophone. Sounds of each type and length category were heard from distant as well as nearby seals so that none of these sounds were characteristic of a particular seal.

A second type of underwater sound which we associate with *Histriophoca* was a broadband puffing sound with frequencies below 5 kHz and lasting a little less than 1 s (Figure 3). This was somewhat reminiscent of some seal respiratory sounds, but it was not audible in air and we could not correlate them with respiratory activity. The puff sounds were 20 to 25 dB lower level than the sweeps.

Discussion

The downward sweeping frequency and pulsed quality of the sounds is characteristic of many underwater calls of other seals: *Erignathus barbatus* (Ray et al. 1969), *Leptonychotes weddelli* (Ray 1967; Schevill and Watkins 1965, 1971), *Pagophilus groenlandica* (Watkins and Schevill in prep.), *Pusa hispida* (Stirling 1973), *Arctocephalus philippii* (Norris and Watkins 1971). Coincident with spring reproductive activities, most of these pinnipeds produce striking underwater acoustic signals and greatly increase their calling. Ovulation normally occurs from mid-April to mid-May in *Histriophoca* and adult males remain sexually potent through early June (Burns[3]). Analogy to these other pinnipeds suggests similar social functions for the underwater sounds of *Histriophoca,* in reproductive and/or territorial behavior.

[3]Burns, J. J. 1969. Seal biology and harvest. Marine Mammal Investigations. Fed. Aid Completion Rep., Alaska Dep. Fish Game 10:1-25.

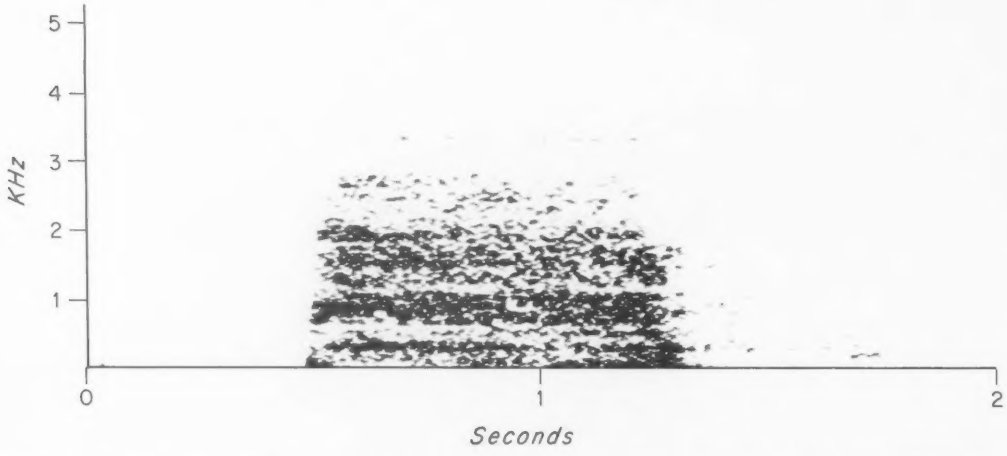

FIGURE 3.—The "puffing" sound of *Histriophoca* is not related to any respiratory activity but is an underwater sound with broadband characteristics that are quite variable. Analyzing filter was 45 Hz.

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WILLIAM A. WATKINS

Woods Hole Oceanographic Institution
Woods Hole, MA 02543

G. CARLETON RAY

Department of Pathobiology
The Johns Hopkins University
615 North Wolfe Street
Baltimore, MD 21205

OBSERVATIONS ON FEEDING, GROWTH, LOCOMOTOR BEHAVIOR, AND BUOYANCY OF A PELAGIC STROMATEOID FISH, *ICICHTHYS LOCKINGTONI*

Stromateoid fishes (Order Perciformes) occur in either coastal or oceanic regions of the sea. Inhabitants of the latter region are generally rare and sporadic in occurrence, especially as adults. Many of the oceanic species have particular adaptations for pelagic existence (Horn 1975) and their frequent association with floating objects, especially coelenterates (scyphomedusae and siphonophores), is well documented (e.g., Mansueti 1963; Haedrich 1967; Bone and Brook 1973; Horn 1975).

The live capture and successful laboratory maintenance of a juvenile *Icichthys lockingtoni* Jordan and Gilbert (family Centrolophidae), an oceanic fish of the North Pacific, provided the first opportunity to record the feeding, growth, and locomotor behavior of this pelagic stromateoid and, upon the death of the fish, to measure its buoyancy and lipid content (as a factor in buoyancy). In this paper, the laboratory rearing and maintenance of oceanic stromateoids are briefly reviewed, and the adaptive strategy of *I.*

lockingtoni for locomotion and buoyancy in the open ocean is compared with that of another pelagic centrolophid, *Schedophilus medusophagus* Cocco.

Materials and Methods

One *I. lockingtoni* was captured during an open-water skin and scuba diving operation conducted from the RV *Nautilus* in the San Pedro Channel (lat. 33°30'N, long. 118°30'W) off southern California on 24 October 1974. The fish was approached by a scuba diver at a depth of 11 m as it swam slowly beneath a scyphozoan medusa (tentatively identified as a member of the family Pelagiidae) approximately 30 cm in bell diameter. The specimen was captured in a 1-liter jar, placed in a container filled with aerated seawater aboard the ship and transported to the laboratory at California State University, Fullerton, where it was placed in a 95-liter Instant Ocean[1] Tank. Approximately 6 h lapsed between time of capture and placement of the fish in the laboratory tank. Sea temperature at the depth of capture was 15°C and the temperature of the seawater in the tank when the fish was introduced was 13°C. Temperature of the seawater in the tank during the maintenance period ranged from 8.8°C to 22.2°C ($\bar{x}$ ± 1 SD = 14.9 ± 2.2°C) and the salinity from 35.0‰ to 37.5‰ (35.7 ± 2.3‰).

The fish began feeding regularly on 7 November 1974 and was fed daily (except for 8 days, irregularly spaced, when feeding was not possible) by hand with measured amounts of frozen brine shrimp (90% water content). The fish took the food at the surface so that it was possible to keep an accurate record of the amount of food it ingested. The daily diet of frozen brine shrimp ranged in weight from 1.2 to 8 g (0.4–1.4 g dry wt/100 g live wt fish). The feeding rate was based on the amount the fish would consume immediately. Weight and standard length (SL) of the specimen were recorded on 7 November and at irregular intervals throughout the maintenance period by removing the fish in a tray from the tank and placing it on a platform balance beside a metric rule. The weighing and measuring procedure required that the fish be out of water a maximum of 15 s. The conversion of food into fish flesh was obtained by dividing the food intake (dry wt) by the gain in weight of the fish (wet wt) (Hastings and Dickie 1972).

Locomotor behavior was recorded from periodic observations and from analysis of an 8-mm ciné film made of the fish swimming in the tank.

Buoyancy of the specimen was measured immediately after its death (7 April 1975) by weighing it in air and in water of known temperature and salinity. Results were expressed as the percent of the weight in air that the fish weighed in seawater.

After the buoyancy determination the specimen was frozen and later thawed for lipid analysis. Total lipids of the spine, skull, viscera, and flesh (all other tissues) were extracted with chloroform-methanol (2:1, vol/vol) and expressed for each of the four body parts as the percent of total body lipid and as the percent of dry weight of that body part.

Results

The specimen of *I. lockingtoni* became conditioned within 1 wk of capture to take food directly from the hand. Chunks of frozen brine shrimp offered at the surface were quickly approached and usually taken in a single bite. Throughout the maintenance period, the fish occasionally swam upside down, apparently a normal mode of swimming, and sometimes fed in this position. The fish also bit at other available objects in the tank, including human fingers at feeding time, grasping them and then rolling and twisting its body as if to tear free the objects. Vision appeared to be the primary sense used in locating food.

The specimen measured 105 mm SL at the time of capture. On 7 November, when the fish began to feed regularly and the record of food intake and growth was begun, the fish weighed 30.6 g and was 115 mm SL (Table 1). The specimen lived 165 days, until 7 April 1975, when the temperature of the tank increased unexpectedly to 26°C apparently causing death. At death, the fish weighed 54.5 g (78.1% increase over its 7 November weight) and had grown to 168 mm SL (46.1% increase). Its weight peaked on 5 February at 64.6 g then declined to the final value.

During the 151-day period (7 November-7 April), 65.7 g (dry wt) of frozen brine shrimp were ingested by the fish (Table 1). Based on this intake and the weight gain recorded (23.9 g wet wt), the overall conversion factor was 2.7. For the 90-day

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Size, food intake, and food conversion, at cumulative intervals, of *Icichthys lockingtoni* maintained in the laboratory over a 151-day period.

Date	Fish length (mm SL)	Fish weight (g wet wt)	Food intake[1] (g dry wt)	Conversion factor (food intake ÷ fish wt gain)
7 Nov. 1974	115	30.6	—	—
22 Nov. 1974	120	33.8	3.8	1.2
14 Dec. 1974	125	36.5	11.7	2.0
4 Jan. 1975	135	43.2	21.2	1.7
5 Feb. 1975	—	64.6	38.9	1.1
7 Apr. 1975	168	54.5	65.7	2.7

[1]Based on 90% water content.

period ending on 5 February when the fish's weight reached a maximum, *I. lockingtoni* ingested 38.9 g of food (dry wt) and gained 34.0 g (wet wt) for a food conversion of 1.1.

The fish swam slowly and continuously most of the time but infrequently hovered in one position. The short (12.6% SL, 168 mm SL), fanlike pectoral fins were the primary propulsive elements when the fish cruised slowly in the tank. Each pectoral fin was flapped in a semirotary manner, alternately to the opposing fin, at approximately 1 stroke/s. At short-term increased speeds, the pectoral fins were held against the body and thrust obtained by sinuous movements of the posterior trunk and caudal region. The small (6.5% SL, 168 mm SL) pelvic fins were actively used during swimming especially in braking and turning. As mentioned, the fish was adept at swimming for short distances upside down and at other attitudes about its longitudinal axis.

The weight of the fish in seawater (20°C, 33‰) immediately after death was 0.36 g or 0.66% of its weight in air (slight negative buoyancy).

Lipids constituted 4.9% of the dry weight of the spine, 10.6% of the skull, 17.0% of the viscera, and 4.4% of the flesh. Spine lipids made up 2.2% of the total body lipids, skull lipids 2.9%, visceral lipids 35.3%, and flesh lipids 59.6%.

Discussion

The stromateoid characteristic of associating with pelagic coelenterates as juveniles is particularly well developed in *I. lockingtoni*. Many of the small (<200 mm SL) specimens captured have been taken with medusae (Fitch 1949; Haedrich 1966; Fitch and Lavenberg 1968). The locomotor behavior and feeding behavior of *Icichthys* recorded in this report are traits well suited for living with medusae. The ability to swim at various attitudes about the longitudinal axis and to hover and maneuver using the paired fins would be advantageous in moving among and avoiding the stinging tentacles of medusae. The grasping of large objects followed by a rolling and twisting of the body appears to be a feeding pattern especially appropriate for tearing chunks from the tentacles and other tissues of coelenterates. Haedrich (1966) reported that the stomachs of *Icichthys* often contain siphonophore remains. A feeding behavior also consisting of grasping objects and twisting the body has been observed (R. L. Haedrich pers. commun.) in two other pelagic centrolophids, *Hyperoglyphe perciforma* (Mitchill) and *Schedophilus medusophagus*.

The food conversion values for *Icichthys* of 2.7 for the 151-day period and 1.1 for the initial 90-day period are comparable to or, in the latter case, more efficient than average total conversions (1.75-2.7) reported by Phillips (1972:19) for brook trout and brown trout fed a variety of diets at temperatures ranging from 8.3° to 15.6°C. The feeding rates of 0.4-1.4% for *I. lockingtoni* were lower than those of 2-3% at which maximum conversion occurred in channel catfish (Tiemeier et al. 1969). Useful comparisons between different experiments and different species are limited since a variety of physical and biological factors influence energy requirements and conversion efficiencies and since food conversions, as calculated here, are less meaningful and often different from caloric conversions (Phillips 1972). The most important result of the present study, however, is that the conversion efficiency of *I. lockingtoni* did change, generally declining with age of the fish (see below).

Limited success has been achieved in maintaining pelagic stromateoids in the laboratory. Maul (1964) recorded rapid growth in two species of centrolophids *Schedophilus* (= *Mupus*) *maculatus* and *Schedophilus* (= *Mupus*) *ovalis*, fed on a diet of shrimp in a large (700-liter) aquarium. The former species increased in weight from 7 to 95 g in 61 days, and *S. ovalis* increased in length from 100 to 198 mm SL over the same period. R. L. Haedrich (pers. commun.) has kept two other centrolophids, *S. medusophagus* and *Hyperoglyphe perciforma*, for 2- to 3-mo periods in small (40- to 100-liter) tanks at Woods Hole Oceanographic Institution. D. Gruber at the Southwest Fisheries Center in La Jolla has hatched and reared a series of larvae of *I. lockingtoni* (E. H. Ahlstrom pers. commun.). One larva that hatched on 12 June 1975 at a notochord length of 3 mm grew to 90 mm SL by 30 August 1975 (80 days).

The rare and sporadic live capture of stromateoids prevents the development of appropriate procedures for long-term maintenance. To date, maintenance trials indicate (pers. obs.; R. L. Haedrich pers. commun.) that the fishes will grow rapidly for short periods but then lose interest in feeding and gradually decline in health, especially as the adult stage is reached when pelagic stromateoids generally change their mode of life and occupy greater depths. The initial growth and high conversion efficiency followed by the reduced growth and lowered efficiency of *I. lockingtoni* are consistent with these observations.

The apparent adaptive strategy for pelagic existence of juvenile *I. lockingtoni* involving locomotor behavior, buoyancy, and lipid content parallels that described (Bone and Brook 1973) for juvenile (85-200 mm SL) *Schedophilus medusophagus* from the North Atlantic. There is no swim bladder in either species in this size range, the lipid content of both is low and both species are slightly negatively buoyant (weight in water 0.35-0.53% of weight in air for *S. medusophagus*). In each case, the pectoral fins are important in generating both thrust and lift.

The two species also appear to undergo similar changes in mode of life as the adult stage (about >200 mm SL) is reached and the fishes become independent of floating objects and occupy greater depths in the water column. Data, particularly on adult *S. medusophagus*, indicate that certain density reducing mechanisms (increase in lipid and water content, decrease in dense tissues, i.e., muscle and bone) are more prominent than in the juvenile stage. Horn (1975) found that a large (285 mm SL) specimen of *S. medusophagus* was neutrally buoyant, swam in a slow, near-anguilliform manner and had relatively small pectoral fins of minor importance in generating thrust and lift. Lipid content in the same specimen was relatively high, especially in the bones (spine 23% and skull 21% lipid by dry wt) (Lee et al. 1975).

Data are yet insufficient on adult *I. lockingtoni* to fully demonstrate parallel strategies in the two species. The relative length of the paired fins of *Icichthys*, however, decrease with age (Haedrich 1966) at a rate and magnitude similar to that in *S. medusophagus*. In addition, the muscles of large (270 mm SL) *Icichthys* are soft and loosely packed as in *Schedophilus*. Data on buoyancy and lipid content of adult *I. lockingtoni* are needed to test the hypothesis.

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MICHAEL H. HORN

Department of Biology
California State University
Fullerton, CA 92634

BODY SIZE AND LEARNED AVOIDANCE AS FACTORS AFFECTING PREDATION ON COHO SALMON, *ONCORHYNCHUS KISUTCH*, FRY BY TORRENT SCULPIN, *COTTUS RHOTHEUS*

Wild coho salmon juveniles, *Oncorhynchus kisutch*, in Washington streams range in fork length (FL) from about 30 mm at the time of emergence from the gravel to 120 mm on migration to the sea. Predation by sculpins, *Cottus* spp., is limited to the smaller salmon; few salmon >45 mm FL have been recovered from the stomachs of sculpins (Patten 1962, 1971a, 1972). Yet, sculpins are capable of eating hatchery reared fall chinook salmon, *O. tshawytscha*, of 60 mm FL (Patten 1971a). Apparently, the reason sculpins do not normally prey on wild coho salmon >45 mm FL is not entirely dependent on the relative sizes of prey and predator.

The present study is on the ability of torrent sculpin, *C. rhotheus*, to prey on coho salmon >45 mm FL, as well as the predator avoidance behavior of coho salmon to torrent sculpins in stream aquaria adjacent to the Cedar River near Ravensdale, Wash., during 1965 and 1966. One experiment indicates the absolute size of coho salmon that can be caught, subdued, and swallowed by a torrent sculpin of a given length. The other suggests that coho salmon previously exposed to torrent sculpins become less susceptible to these predators in future interactions.

Facilities and Procedures

Two related studies—one on predator-prey size relations and the other on the learned predator avoidance ability of coho salmon prey—were conducted in stream and holding aquaria that received water from the Cedar River. The two stream aquaria were 2.4 m long, 0.6 m wide, and 0.6 m high; water depth ranged from 2 to 18 cm. The eight holding aquaria were 34 cm wide, 41 cm long, and 36 cm high; water depth was 18 cm (a more complete description of the experimental facilities is given by Patten 1971b).

Water was gravity fed from a low level dam on the Cedar River to a head box through a flume and then to the aquaria. Each aquarium received a continuous supply of clear water; temperatures in the morning during the study ranged from 4.4° to 12°C.

Torrent sculpins were collected by electrofishing in Soos Creek, King County, Wash., and coho salmon were seined in upper Rock Creek of the Cedar River drainage. It was assumed that the state of hunger of all torrent sculpins was similar, that the coho salmon had little experience with fish predators, and that this experience was similar for all subjects. The assumption for the coho salmon was probably valid because the only other common species of fish at the seining site was the shorthead sculpin, *C. confusus*—a relatively nonpredaceous species of fish (unpubl. studies of author). Furthermore, the few individuals of the shorthead sculpin observed were small.

The effect of predator-prey length relations on predation was determined from 23 tests where six coho salmon of a given length group were available to four torrent sculpins of a given length group (Table 1) for 4 days. The test procedure was to collect torrent sculpins the first day and place them in a holding aquarium without food; on the second day, coho salmon were collected and six individuals within 5 mm of a given length were placed in a holding aquarium; on the third day, four torrent sculpins within 5 mm of a given length were introduced into the holding aquarium containing the coho salmon; 4 days later, the number of coho salmon eaten was recorded and the experimental fish were discarded. The largest available size group of torrent sculpins used was 120 mm total length (TL).

TABLE 1.—Results of 23 tests where six coho salmon of a length group were subjected to predation by four torrent sculpins of a length group. Predation on one or more coho salmon is denoted by P and no predation by N.

Total length of sculpin (mm)	Fork length of salmon (mm)						
	40	50	60	70	80	90	100
60	–	P	N	–	–	–	–
80	P	P	P	N	–	–	–
80	–	P	N	–	–	–	–
100	–	–	P	P	N	–	–
100	–	–	P	N	–	–	–
100	–	–	–	N	–	–	–
120	–	–	P	P	P	N	N
120	–	–	–	–	N	N	N
120	–	–	–	–	P	–	–

The ability of coho salmon to learn to evade predation was tested by comparing the relative survival of naive coho salmon (those which had not been exposed to torrent sculpin predators) with coho salmon conditioned to predation by the torrent sculpin. Coho salmon were conditioned by placing 20 individuals into a stream aquarium with eight torrent sculpins. Some of those that had survived a 48-h association with torrent sculpins

were maintained in holding aquaria without torrent sculpins for 24 h before being subjected to predation in test conditions. Two types of test groups, each consisting of 20 coho salmon (per stream aquarium), were used. In the naive group, all coho salmon were naive; in the naive and conditioned group, 10 naive and 10 conditioned fish were tested together.

The procedure for testing naive coho salmon was to collect torrent sculpins and place them in holding aquaria without food; on the second day, coho salmon were collected and 20 individuals, 37 to 42 mm FL, were placed in each stream aquarium; on the third day, 10 torrent sculpins, 83 to 127 mm TL, where lengths averaged about 100 mm per test group, were transferred from the holding aquarium to each stream aquarium. Forty-eight hours later, the surviving coho salmon were counted and experimental fish were discarded.

The procedure for testing the naive and conditioned group of coho salmon was similar to the foregoing test procedure except that on the second day, 10 naive coho salmon were collected and placed in each stream aquarium with 10 conditioned coho salmon. The tip of a ventral fin of the conditioned coho salmon was clipped at the time they were introduced into the stream aquarium to allow them to be recognized at the end of the test. Thus, if there was an adverse effect from clipping, it would be on the group with the greater expected survival. Eight replicate tests were made on each of the two conditions.

Length Relation

The experimental procedure placed the coho salmon in close proximity to torrent sculpins for a prolonged period to enhance the possibility of predation. Torrent sculpins responded to this opportunity by preying on larger coho salmon than has been observed in nature (Table 1). The maximum size of coho salmon a torrent sculpin is capable of preying upon is probably limited by the physical size of a coho salmon that a torrent sculpin can catch, subdue, and swallow. While the swimming ability is probably greater for larger coho salmon, this may not be too important because predation by torrent sculpins is accomplished by ambush rather than by pursuit. Torrent sculpins under natural conditions rarely eat coho salmon 40 to 80 mm FL, indicating that some factor of coho salmon behavior must decrease their susceptibility to predation.

Predator Avoidance Response

The average survival of the naive group consisting only of naive fish was 45.5%; within the naive and conditioned group, consisting of conditioned and naive coho salmon tested together, the naive fish had a 71% survival, and the conditioned coho salmon had a 75% survival. Cumulative chi-square tests of homogeneity showed no significant differences within the naive test group or within the naive and conditioned group (Table 2). The Z test showed no significant difference between the conditioned and naive coho salmon that were tested together ($Z_{P0.05} = +0.53 < 1.645$). There was, however, a significant difference between the group consisting of naive coho salmon only and the group consisting of naive plus conditioned coho salmon ($Z_{P0.05} = +5.29 > 1.645$).

Mortalities of coho salmon were significantly reduced by conditioning; also, naive fish tested with conditioned fish behaved as conditioned fish. The results of these tests are probably due to rapid conditioning of the coho salmon and a transferable predator avoidance reaction. Rapid conditioning was evident because conditioning of fish to a stimulus other than predators is usually accomplished only after many trials. Conditioning coho salmon to evade predation by exposing them to torrent sculpins probably reinforces a strong innate avoidance behavior. In another case, rapid conditioning of sockeye salmon, *O. nerka*, to evade predation by rainbow trout, *Salmo gairdneri*, has been demonstrated by Ginetz and Larkin (1976). Experiments by Russians have shown that certain fishes, including the chum salmon, *O. keta*, increased their ability to evade predation after a 2- to 4-day training period with predators (Kanid'yev et al. 1970).

TABLE 2.—Comparative survival of two groups of coho salmon that were exposed to predation by the torrent sculpin. One group consisted of naive fish only and the other consisted of naive and conditioned coho salmon combined. The initial number of coho salmon per group per stream aquarium was 20.

Naive group		Naive and conditioned group			
		Naive		Conditioned	
No. of fish	Survivors	No. of fish	Survivors	No. of fish	Survivors
20	6	10	7	10	9
20	12	10	9	10	10
20	12	10	6	10	6
20	7	10	7	10	9
20	8	10	5	10	8
20	10	10	7	10	6
20	12	10	9	10	7
20	6	10	7	10	5

A transferable predator avoidance reaction may account for the conditioned and naive coho salmon acting as a homogeneous group in the present study. Conditioned coho salmon had learned to avoid torrent sculpins through some unknown mechanism. Apparently the naive fish behaved as conditioned individuals through visual clues resulting in mimicry. O'Connell (1960) noted mimicry in sardines in a conditioned response experiment where unconditioned replacement fish performed in unison with the school of conditioned fish from the first trial. Kanid'yev et al. (1970) indicated that the consensus of Russian workers was that sight played the main role in developing the predator avoidance reaction and that reinforcement is maximal for fish that are observers.

Sculpins commonly cohabit streams with and prey on young salmon. Growth of salmon to a size too large for sculpins to successfully prey on effectively removes them from this predator predation. The maximum size of coho salmon that a torrent sculpin can catch and eat in laboratory conditions is much larger than those that are normally preyed upon in nature. This indicates that although growth is effective in limiting torrent sculpin predation on coho salmon, other factors are equally important. Among salmon, the coho has a well-developed innate predator avoidance response (Patten 1975). The response apparently can be reinforced by experience with fish predators and this conditioning probably increases their early survival in streams.

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BENJAMIN G. PATTEN

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112

DESCRIPTION OF MEGALOPA OF SNOW CRAB, *CHIONOECETES BAIRDI* (MAJIDAE, SUBFAMILY OREGONIINAE)

Chionoecetes bairdi Rathbun, a brachyuran crab, occurs on the continental shelf from Puget Sound in Washington State, northward into the Bering Sea, and westward along the Aleutian Islands. The species has been taken as deep as 474 m (Garth 1958), but adults commonly occur at depths less than 190 m. *Chionoecetes bairdi* may be quite abundant in inshore areas throughout its range and has become an important subsistence and commercial species because of its large size and accessibility. It supports an extensive fishery in the Bering Sea and Gulf of Alaska for three nations—the United States, the Soviet Union, and Japan.

The range of *C. bairdi* overlaps that of three other species of *Chionoecetes: C. tanneri* Rathbun, *C. angulatus* Rathbun, and *C. opilio* (O. Fabricius). *Chionoecetes tanneri* ranges from Mexico north to the State of Washington, and commonly occurs between 370 and 1,630 m on the outer slopes of the continental shelf (Garth 1958). *Chionoecetes angulatus* occurs throughout the range of *C. bairdi*, but *C. angulatus* occurs on the lower slopes of the shelf edge between 730 and 2,980 m (Garth 1958). *Chionoecetes opilio* occurs only in the Bering Sea, and its distribution is often sympatric with *C. bairdi*. Two other species of *Chionoecetes* occur in the western Pacific Ocean,

C. japonicus (Rathbun) and *C. opilio elongatus* Rathbun.

Since *C. bairdi* has become commercially important, its biology and distribution are receiving more attention. Descriptions of the larvae for *C. bairdi* and *C. opilio* are important because both are taken commercially and their distribution overlaps. Haynes (1973) described prezoeae and stage I zoeae of *C. bairdi* (and *C. opilio*), but stage II zoeae and megalopa have not been described.

In this paper we describe megalopa of *C. bairdi* and compare them with megalopa of *C. opilio* (Motoh 1973) and *C. opilio elongatus* (Kurata 1963b)—the only other *Chionoecetes* species for which the megalopal stages have been described.

There seems to be some lack of consistency in the literature concerning the singular and plural of the megalopal stage. The original singular was called megalops, because of the large and prominent eyes. Many authors (e.g., Kurata 1963a, b; Makarov 1967; Motoh 1973) have changed this to megalopa for both singular and plural. Others (e.g., Hart 1960; Poole 1966) have latinized megalopa in the plural to megalopae. In this manuscript both singular and plural of the megalopal stage will be referred to as megalopa since this is more widely accepted.

Methods and Materials

About 50 larvae[1] of *C. bairdi* were taken from Fish Bay near Sitka, Alaska, at lat. 57°22′N, long. 135°33′W on 14 April 1971. They were caught with 70-cm-diameter nylon bongo nets towed 8 to 9 m below the surface; mesh sizes of the nets were 0.505 and 0.333 mm. The larvae were held in a 3-liter aquarium supplied with continuous-flowing filtered seawater. The aquarium was transferred from the research vessel to the laboratory on 19 April. The water temperature fluctuated between 8° and 10°C on the vessel and 6.3° and 6.9°C in the laboratory. The *C. bairdi* larvae fed upon other zooplankton caught during the same tow until that food was gone. By then, it appeared all the larvae were at the megalopal stage, and we began feeding them finely chopped herring. Some megalopa were preserved on 19 April in 5% formaldehyde and seawater. Their identification as *C. bairdi* was confirmed by raising the remaining megalopa to the juvenile stage (maximum carapace width 13.9 mm) and comparing them with the juvenile morphology described by Garth (1958).

Megalopal larvae identical morphologically to those we had raised were collected in a vertical plankton haul on 21 May 1973, at the entrance to Resurrection Bay south of Seward, Alaska, at lat. 59°48′N, long. 149°30′W. These specimens were dissected and used as the basis for our illustrations of morphology, appendage setation, and other characteristics.

Illustrations (Figure 1) were prepared with the aid of a camera lucida. An ocular micrometer was used to measure body dimensions of nine of the preserved specimens. The measurements were 1) carapace length (two measurements had to be taken because the rostral tip was often damaged—straight-line distance from rostral tip to posterior median margin of carapace and straight-line distance from the notch between rostral and preorbital spine to posterior median margin of carapace); and 2) carapace width (straight-line distance between widest part of carapace).

To compare our description of megalopal larvae of *C. bairdi* with descriptions of megalopa of other species in the genus, we used our collections from the Chukchi Sea and descriptions by Motoh (1973) for *C. opilio* and descriptions by Kurata (1963b) for *C. opilio elongatus*.

Description of Megalopa

Carapace length 3.12 to 3.48 mm (mean 3.30 mm) inclusive of rostrum and 2.60 to 2.80 mm (mean 2.73 mm) from rostral notch. Carapace width 1.80 to 2.12 mm (mean 1.97 mm).

Carapace triangular shaped and bears seven major processes (Figure 1a-c). Anterior rostral region bears three sharp spines, two preorbital and one rostral. Rostral spine three times length of preorbital spines (measuring from rostral notch) and points ventrally. Frontal and rostral region slightly depressed. Pair of anterolateral spines separated by thin median ridge. Pair of cardiac dorsolateral spines sweep slightly posteriorly. Minute but conspicuous lateral spines occur in region of pterygostomial-branchial ridge. Small ridge along posterolateral margin of carapace bears a wartlike protuberance medially, directly above proximal end of abdomen. Eyes stalked.

[1]The specimens preserved 14 April were lost and could not be examined to determine their stage of development. We believe that they were stage II zoeae or megalopa or a combination of both.

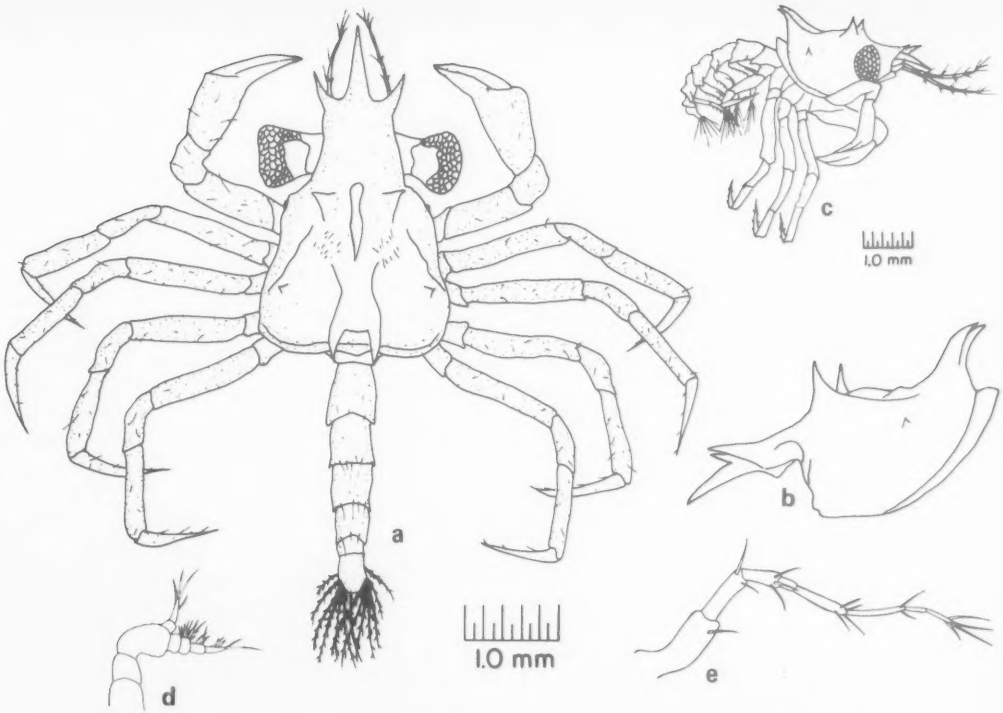

FIGURE 1.—Megalopa of *Chionoecetes bairdi;* antennule and antenna from right side of specimen (a) dorsal view of entire specimen; (b) lateral view of carapace; (c) lateral view of entire specimen; (d) antennule; (e) antenna.

ANTENNULE (Figure 1d)—Three-segmented peduncle has terminal pair of segmented rami. Smaller ramus has two segments. Distal segment has four setae, proximal shorter segment naked. Second terminal ramus has four segments. Number of setae per segment, beginning distally, 5, 3, 10, and 0.

ANTENNA (Figure 1e)—Antenna has eight segments. Setation formula is 4, 0, 2, 4, 0, 3, 2, and 1. Setae located on distal ends of segments.

MANDIBLE (Figure 2a)—Mandibular palp has three segments. Distal segment has about 10 setae; middle and proximal segments naked.

MAXILLULE (Figure 2b)—Endopodite has one hook-shaped segment with two terminal setae. Basipodite has 20-23 coarse plumose setae. Smaller coxopodite has 13-16 coarse plumose setae.

MAXILLA (Figure 2c)—Exopodite (scaphagnathite) outer margin lined with 38 plumose setae. One endite naked and ends in a point. Two endites heavily bifurcated. Lobes of basal endite distally bear 10 and 8 plumose setae, respectively, and lobes of coxal (proximal) endite bear 6 and 10 plumose setae.

FIRST MAXILLIPED (Figure 2d)—Epipodite has eight long hairs. Exopodite is two segmented with six heavily plumose setae; setation formula is 5 and 1. Broad endopodite has three spines on distal end. Basal endite bilobed with 22-29 plumose setae on larger lobe and 11-14 plumose setae on smaller.

SECOND MAXILLIPED (Figure 2e)—Epipodite has three hairs. Exopodite has two segments with five heavily plumose setae on distal segment. Endopodite has four segments; setation formula 9, 4, 1, and 1.

THIRD MAXILLIPED (Figure 2f)—Epipodite well developed with several nonplumose hairs. Exopodite two segmented with five terminal setae. Endopodite has five large segments with numerous spines on all segments; setation formula 8, 15-17, 8-10, 8, and 30-34.

PEREIOPODS (Figures 1a, 2g)—Pereiopods

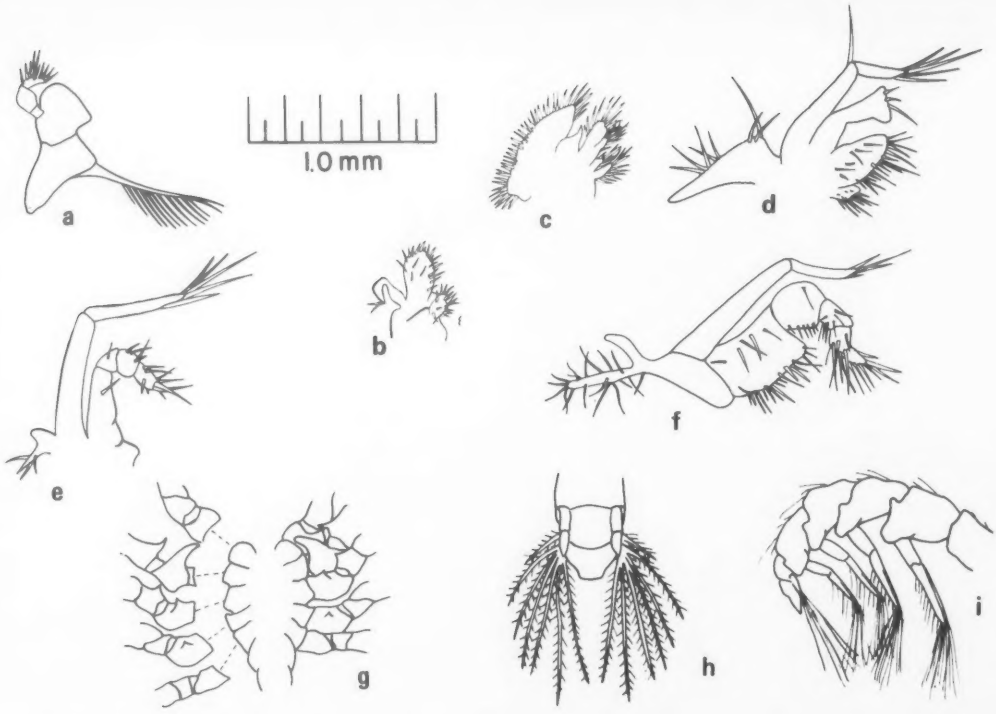

FIGURE 2.—Mouthparts from right side of megalopa of *Chionoecetes bairdi* (a) mandible; (b) maxillule; (c) maxilla; (d) first maxilliped; (e) second maxilliped; (f) third maxilliped; (g) ventral view of sternum and pleopod attachment; (h) ventral view of telson and uropods; (i) lateral view of abdomen.

closely resemble those of adult. Coxopodite and basipodite spines, one each, located ventrally on chelipeds and ambulatory legs except for fourth leg. First ambulatory leg spines especially long. Cheliped and third ambulatory leg spines minute. Dactylopodites of ambulatory legs one, two, and three have conspicuous spine projecting from tip.

ABDOMEN AND TELSON (Figure 2h, i)—Abdomen six segmented. Sixth segment and telson small. No spines present. Segments two through five have long setae on dorsal surface.

PLEOPODS (Figure 2i)—Pleopods present on abdominal segments two through five. A single-segmented endopodite (not shown in figure) arises from proximal segments of each pleopod. Endopodites have four hooked setae on distal end of first three pairs of pleopods and three hooked setae on distal end of last pair of pleopods. Exopodites of pleopods two and three have variable numbers of plumose setae, 15 through 18. Exopodites of pleopods four and five have 17 and 15 plumose setae, respectively.

UROPODS (Figure 2h)—Uropods two segmented and have seven plumose hairs arising from each distal segment.

How to Distinguish Megalopa of *Chionoecetes bairdi*, *C. opilio*, and *C. opilio elongatus*

Megalopa of *C. bairdi* are similar to megalopa of *C. opilio* and *C. opilio elongatus* in major carapace spination and size. The characteristics which separate these species can be determined without dissection. The four most useful characteristics are: 1) *C. bairdi* has a minute lateral spine in the region of the pterygostomial-branchial ridge while the others do not (see Kurata 1963b; Motoh 1973); 2) *C. bairdi* has a more pronounced ridge along the posterior margin of the carapace than *C. opilio* and *C. opilio elongatus* (Kurata 1963b; Motoh 1973); 3) the rostral spine of *C. bairdi* is three times the length of the preorbital spines, whereas the rostral spine on *C.*

opilio is 1.5 to 2.0 times the length of the preorbitals (from our samples from Chukchi Sea); and on *C. opilio elongatus* all three spines are nearly the same length (Kurata 1963b); 4) *C. bairdi* has a rudimentary spine immediately posterior to each eye; in *C. opilio* and *C. opilio elongatus* this spine, though still minute, is quite conspicuous.

Key to Megalopa of Some Common Brachyuran genera of the Northwest

The following key is to provide a means of identification of some common Brachyura megalopa of the northwest to the generic level. As only characteristics which can be determined without dissection have been used, the key should be used for preliminary sorting. The present state of knowledge of these megalopa comes from six sources (i.e., Hart 1960; Kurata 1963a, b; Poole 1966; Makarov 1967; Motoh 1973). Key modified after Makarov (1967).

A. Carapace bears dorsal spines
  B. Posterior part of carapace bears one spine ..... *Hyas; Oregonia; Cancer*
  B′. Posterior part of carapace bears two spines ..... *Chionoecetes*
A′. Carapace bears no dorsal spines
  B. Angles of posterior margin of abdominal somite 5 reach beyond somite 6 ..... *Telmessus*
  B′. Angles of posterior margin of abdominal somite 5 reach to middle of somite 6 ..... *Erimacrus*

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STEPHEN C. JEWETT

Institute of Marine Science
University of Alaska
Fairbanks, AK 99701

RICHARD E. HAIGHT

Northwest and Alaska Fisheries Center Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

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